Characterization of *Erwinia amylovora* - Host Plant and - Biocontrol Agent Interactions

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Table of contents

Summary

Fire blight is caused by the phytopathogenic Gram-negative enterobacterium *Erwinia amylovora* and infests a wide range of commercially, ornamentally and ecologically important members of the Rosaceae family. Fire blight is a devastating necrogenic disease and the damage to apple and pear production is a major concern. The pathogen spreads systemically in host plants after entering through natural openings (nectarthodes, stomata) or wounds. Dependent on the plant part affected, disease symptoms develop as blossom blight, shoot blight or rootstock blight. Until now, no systemic cure for infected plants is known, and diseased tissues have to be removed by pruning. *E. amylovora* overwinters in cankers and following warming temperature emerges as ooze in spring. The ooze consists of bacterial cells and exopolysaccharides produced by the pathogen. The viscous texture of the ooze protects bacterial cells from abiotic stress factors and facilitates dispersal from plant to plant. Pathogenicity of *E. amylovora* to host plants is strictly dependent on a functional type III secretion system and the exopolysaccharide amylovoran. Factors contributing to virulence and ecological fitness of *E. amylovora* are reviewed in **Chapter 2**. Availability of genome sequences in the genus *Erwinia* provides the basis to analyze the full arsenal of critical determinants for virulence, host range and ecological fitness of *E. amylovora*. Preventive disease control measures include the application of the antibiotics streptomycin and oxytetracycline to protect flowers. The emerging resistance of *E. amylovora* to the most effective antibiotic streptomycin raises the need for novel management measures. The application of biocontrol agents can significantly reduce the epiphytic growth of the pathogen. The effectiveness of these agents is based on combined modes of action, e.g.site exclusion, nutrient competition, and antibiotic production. Beside this strategy, apple breeding programs led to the development of cultivars with improved resistance to *E. amylovora*. Nevertheless, the main apple cultivars produced and consumed (e.g., 'Golden Delicious', 'Gala') are highly susceptible to the fire blight disease. The underlying processes leading to resistance or susceptibility of apple to *E. amylovora* are largely unknown and knowledge of these might lead to the development of novel control measures of the disease.

The first aim of this thesis was to elucidate additional virulence factors of *E. amylovora* (**Chapter 3**). Using a comparative genomic approach, three type VI secretion systems (T6SS) of unknown function were identified in *E. amylovora* and characterized. Plant assays showed a moderate contribution of T6SSs to *E. amylovora* virulence. Analysis of transcriptomic data generated by RNA-sequencing from *E. amylovora in vitro* cultures and *in*

planta experiments indicated that the T6SSs influence metabolic processes, chemotaxis and motility of the bacteria.

The second aim was to identify and characterize the antibiotic biosynthesis operon for herbicolin I in *Pantoea vagans* biocontrol strain C9-1 described in **Chapter 4**. Analysis of mutants defective in herbicolin I biosynthesis revealed a gene cluster consisting of ten open reading frames located on the plasmid pPag2. Deficiency in herbicolin I production reduced the biocontrol efficacy of *P. vagans* C9-1 on *E. amylovora*. Prevalence screening of 45 *Pantoea* spp. from biocontrol, environmental, and clinical origins for herbicolin I biosynthetic genes revealed this to be a rare trait among the tested strains.

Chapter 5 addresses the third aim of the presented thesis, the transcriptional response of susceptible apple (*Malus* x *domestica* variety 'Golden Delicious') to *E.amylovora* in order to identify genes and pathways affected in the host plant. The data revealed differential expression of genes involved in phytohormone biosynthesis and phenylpropanoid pathways, as well as putative resistance genes, transcription factors and pathogenesis-related genes. In addition, previously unrecognized genes in the apple genome sequence and potential new open reading frames in apple and peach (*Prunus persica*) were identified.

The data presented in this thesis provides a comprehensive knowledge of the T6SSs in *E. amylovora,* focusing on their effects on virulence and the identification of a potential T6SS regulome. The identified gene cluster for the antibiotic herbicolin I in *P. vagans* C9-1 will facilitate the screening process for novel biocontrol agents producing this effective antibiotic. The transcriptional responses revealed by RNA-seq of susceptible apple to *E. amylovora* provide a profound knowledge of this host-pathogen interaction and a basis for the development of novel fire blight control measures.

Zusammenfassung

Feuerbrand wird durch das Gram-negative Bakterium *Erwinia amylovora* verursacht und befällt ein breites Spektrum an Zierpflanzen, der kommerziell und ökologisch wichtigen Mitgliedern der Rosaceae Familie. Feuerbrand ist eine verheerende nekrogene Krankheit deren Schäden ein zentrales Problem für die Apfel- und Birnenproduktion darstellen. Das Pathogen verbreitet sich systemisch in Wirtpflanzen, nachdem es durch natürliche Öffnungen (Nektarien, Stomata) oder Wunden eingedrungen ist. Abhängig davon welcher Pflanzenteil betroffen ist, entwickeln sich die Symptome als Blütenbrand, Sprossbrand oder Wurzelstockbrand. Bis lang ist kein systemisches Pflanzenschutzmittel bekannt, daher müssen erkrankte Pflanzenteile durch Rückschnitt entfernt werden. *E. amylovora* überwintert in Cankern und tritt nach ansteigenden Temperaturen im Frühjahr als Schleim aus. Dieser Schleim besteht aus Bakterienzellen und Exopolysachariden, die vom Pathogen gebildet werden. Dieser zähflüssige Schleim schützt die bakteriellen Zellen vor abiotischen Stressfaktoren und erleichtert ihre Verbreitung von Pflanze zu Pflanze. Die Pathogenität von *E. amylovora* auf Wirtspflanzen ist strikt an ein funktionelles Typ III Sekretionssytem und das Exopolysacharid Amylovoran gebunden. Faktoren die zur Virulenz und ökologischen Fitness beitragen sind detailiert in **Kapitel 2** beschrieben. Die Verfügbarkeit von Genomsequenzen der Gattung *Erwinia* bietet eine fundierte Basis, um alle entscheidenden Determinanten der Virulenz, des Wirtsspektrums und der ökologischen Fitness zu analysieren. Präventive Massnahmen, um Blüten vor Befall zu schützen, beinhalten die Applikation der Antibiotika Streptomycin und Oxytetracyclin. Die aufkommende Resistenz von *E. amylovora* gegen das effektivste Antibiotikum Streptomycin erfordert neue Kontrollmaßnahmen. Die Applikation von Biokontrollorganismen kann das epiphytische Wachstum des Pathogens signifikant reduzieren. Die Wirksamkeit dieser Organismen beruht auf einer Kombination von Wirkmechanismen, wie z.B. Nischenbesetzung (Verdrängung), Konkurrenz um Nährstoffe und Antibiotika-Produktion. Neben diesen Strategien führten Apfelzüchtungsprogramme zur Entwicklung von Sorten mit erhöhter Resistenz gegen *E. amylovora*. Die hauptsächlich angebauten Apfelsorten (z.B. ‘Gala’, ‘Golden Delicious’) anfällig für Feuerbrand. Die zugrunde liegenden Prozesse, die zur Resistenz oder Anfälligkeit von Apfelpflanzen führen, sind weitgehend unbekannt und Erkenntnisse darüber könnten zur Entwicklung neuartiger Bekämpfungsmaßnahmen führen.

Das erste Ziel dieser Arbeit war es, weitere Virulenzfaktoren von *E. amylovora* zu finden (**Kapitel 3**). Durch einen vergleichenden Genomik-Ansatz wurden drei Typ VI

Sekretionssysteme (T6SS) mit unbekannter Funktion in *E. amylovora* identifiziert und charakterisiert. Pflanzenversuche zeigten einen moderaten Beitrag der T6SSs zur Virulenz von *E. amylovora*. Die Analyse von Transkriptomdaten, die durch RNA-Sequenzierung von *E. amylovora in vitro* Kulturen und *in planta* Experimenten generiert wurden, deutete darauf hin, dass die T6SSs Stoffwechselprozesse, Chemotaxis und Motilität der Bakterien beeinflussen.

Das zweite Ziel dieser Arbeit war die Identifizierung und Charakterisierung des Antibiotikum Biosyntheseoperons für Herbicolin I in *Pantoea vagans* C9-1 (**Kapitel 4**). Durch die Analyse von Herbicolin I Mutanten wurde ein Gen-Cluster identifiziert, der aus zehn offenen Leserastern besteht und auf dem Plasmid pPag2 liegt. Das Fehlen der Herbicolin I Biosynthese reduziert die Biokontrollwirkung von *P. vagans* C9-1 auf *E. amylovora*. Ein Screening von 45 biokontroll-, ökologischen und klinischen *Pantoea* Stämmen zeigte, dass die Herbicolin I Produktion eine seltene Eigenschaft unter den getesteten Stämmen ist.

Kapitel 5 befasst sich mit dem dritten Ziel dieser Doktorarbeit: dem Studium der transkriptionellen Antwort anfälliger Apfelpflanzen (*Malus* x *domestica*, Varietät 'Golden Delicious') auf die Infektion durch *E. amylovora*, mit dem Ziel Gene und Stoffwechselwege zu identifizieren, die beeinflusst werden. Die Daten zeigten die differenzielle Expression von Genen, die zu den Phytohormon- und Phenylpropanoid- Signalwegen gehören, sowie von putativen Resistenzgenen, Transkriptionsfaktoren und Pathogenesis-related Genen. Darüber hinaus konnten vormals unerkannte Gene in der Apfelgenomsequenz und potentiell offene Leseraster in Apfel und Pfirsich (*Prunus persica*) identifiziert werden.

Die Daten dieser Doktorarbeit liefern umfangreiche Erkenntnisse der T6SS in *E. amylovora,* speziell über deren Einfluss auf die Virulenz und der Identifikation eines potenziellen T6SS Reguloms. Die Identifizierung des Biosyntheseoperons für das Antibiotikum Herbicolin I in *Pantoea vagans* C9-1 wird den Screening Prozess neuer Biokontrollorganismen, welche dieses effektive Antibiotikum produzieren, erleichtern. Die transkriptionellen Antworten von anfälligen Apfelpflanzen auf *E. amylovora*, welche durch die Daten der RNA-seq identifiziert wurden, liefern umfangreiche Erkenntnisse dieser Wirts-Pathogen Interaktion und eine fundierte Basis für die Entwicklung neuartiger Massnahmen zur Bekämpfung des Feuerbrandes.

Chapter 1

General Introduction

General Introduction

Erwinia amylovora – causal agent of the fire blight disease

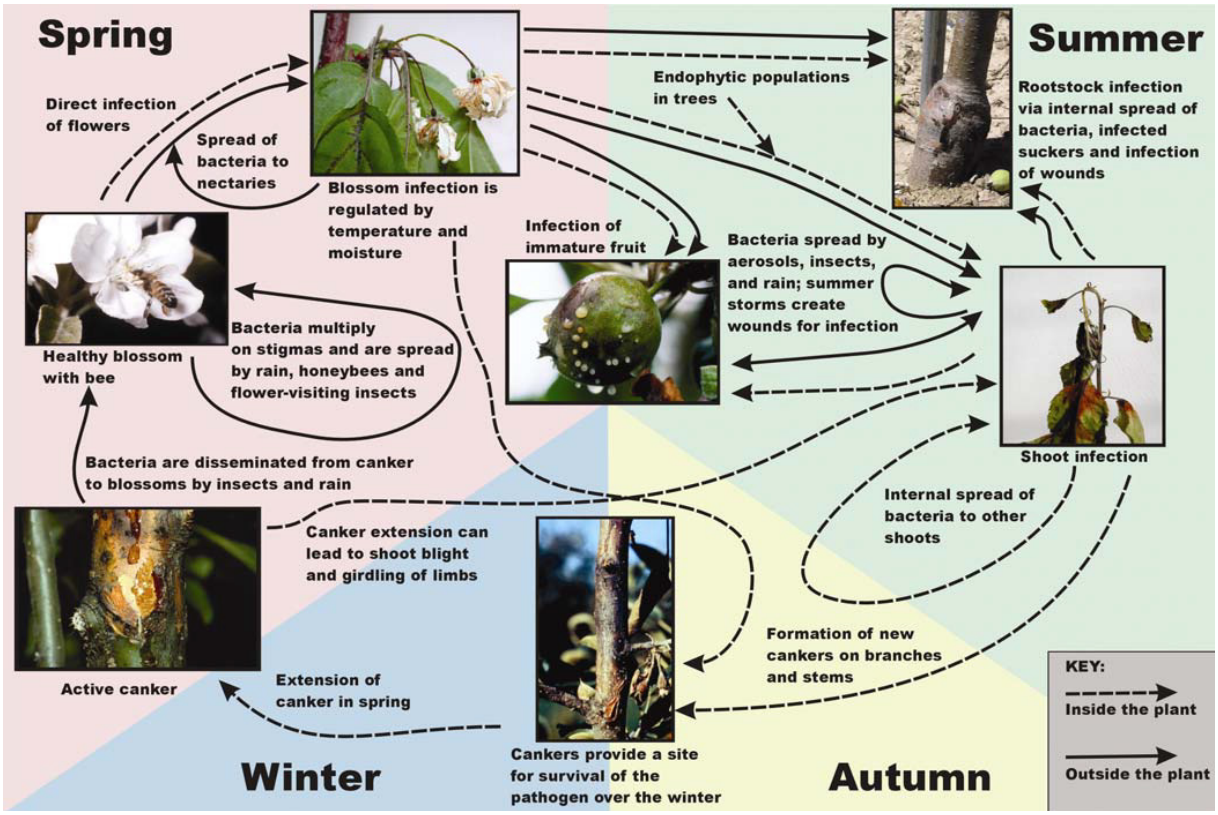
Fire blight, caused by the Gram-negative bacterium *E. amylovora*, is a major disease threat for commercially, ornamentally and ecologically important Rosaceae plants like apple, pear, quince, hawthorn and cotoneaster. The pathogen, first reported in the late 1790s, originated from North America from where it has dispersed to New Zealand in the late 1910s, the United Kingdom and Northern Europe in the late 1950s, and more widely to Europe and the Middle East in the mid-1960s. It continues to spread eastwards across Europe and the Middle East (Jock et al., 2002), threatening Central Asia, the germplasm region of origin for apple and pear. Phytosanitary control measures and the quarantine status of the pathogen (limiting fruit import into fire-blight-free countries) impose high economic losses (Calvin and Krissoff, 1998).

The primary infection sites of the pathogen are opened flowers (via nectarthodes).The pathogen can also invade plant tissue through natural openings (stomata) or wounds, where it spreads systemically through the vascular system. The term fire blight is based on the rapidely developing scorched symptoms. The pathogen can kill trees or entire orchards within a single growing season leading to devastating economic losses (Bonn and van der Zwet, 2000). Dependent on the plant tissue affected, disease symptoms develop as flower necrosis, immature fruit rot, shoot blight (shepherd's crook), and cankers on woody tissues (Fig.1). A characteristic sign of fire blight is bacterial ooze, composed of bacteria and polysaccharides that extrudes from infection sites. Under warming temperatures in spring *E. amylovora* emerges from overwintering cankers and is transferred by crawling insects, rain splashes and from flower to flower by pollinating insects, especially honey bees. Growth of *E. amylovora* on flowers and resulting disease incidence is highly dependent on weather conditions, which has been used to develop disease forecasting models (Billing, 1980).

On the molecular level many important factors contributing to the disease development have been characterized in the last decades. Main virulence factors are effectors delivered by the "hypersensitive response and pathogenicity" (Hrp) type III secretion system (T3SS) and the exopolysaccharide amylovoran (Oh and Beer, 2005). The Hrp-T3SS translocates the effector DspA/E into plant-host cells, where it suppresses cell wall-based defenses (DebRoy et al., 2004). In addition, DspA/E interacts with receptor kinases and with preferredoxin in apple and may therefore function inside the host plant cells (Bonasera et al., 2006; Meng et al., 2006). Besides the Hrp-T3SS, *E. amylovora* posssess further secretion

systems, namely a T1SS, T2SS, two *inv*/*spa*-type T3SS, and three T6SSs (Fig. 2). The T1SS, T2SS, and both the *inv*/*spa*-type T3SS of *E. amylovora* have no role in pathogenicity on immature pear or apple seedlings (Zhang et al., 1999; Zhao et al., 2009).

Figure 1

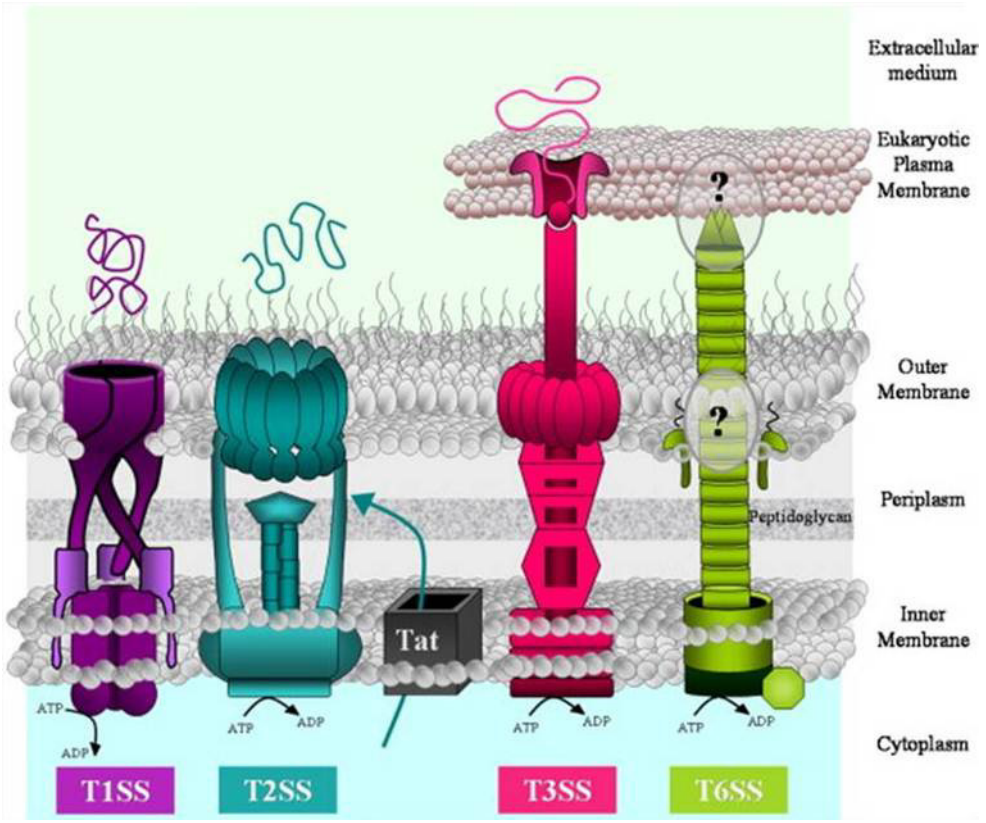


Disease cycle and symptoms caused by *E. amylovora* on host planthost plants (Norelli et al., 2003a).

Chapter 2 reviews these factors and their influence on pathogenicity as well as the genomic, genetic and phylogenetic background of *E. amylovora*. Genome sequencing and comparative genomics approaches identified previously unknown and uncharacterized factors that might contribute to the ecological fitness and virulence of *E. amylovora* CFBP1430 (Smits et al., 2010b). The three type VI secretion systems (T6SS) belong to these factors and were functionally characterized (**Chapter 3**). Since T6SSs have been identified as a protein-secretion system in the human pathogens *Pseudomonas aeruginosa* and *Vibrio cholerae* (Mougous et al., 2006; Pukatzki et al., 2006) various roles could be assigned (Records, 2011) and T6SS loci were identified in many bacterial genomes (Boyer et al., 2009). T6SS clusters consist of a set of 13 core genes and a varying number of accessory genes that differ amongst bacterial genomes (Boyer et al., 2009). The corresponding proteins include IcmF and IcmH (DotU) located in the inner membrane which might interact with cytosolic T6SS subunits

(Cascales, 2008). The AAA+ ATPase, ClpV may energize the assembly of the apparatus and/or secretion of effectors. Additionally, ClpV interaction with the DUF770/DUF877 protein complex is an essential step in T6SS dependent protein secretion (Bönemann et al., 2009). The proteins VgrG and Hcp have been identified as secreted effectors and may as well assemble a T4 bacteriophage tail spike-like puncturing device (Pukatzki et al., 2007; Leiman et al., 2009). Hcp proteins assemble beneath the VgrG protein to form a tube that breaches the outer membrane and delivers effectors to the extracellular space (Fig. 3).

Figure 2

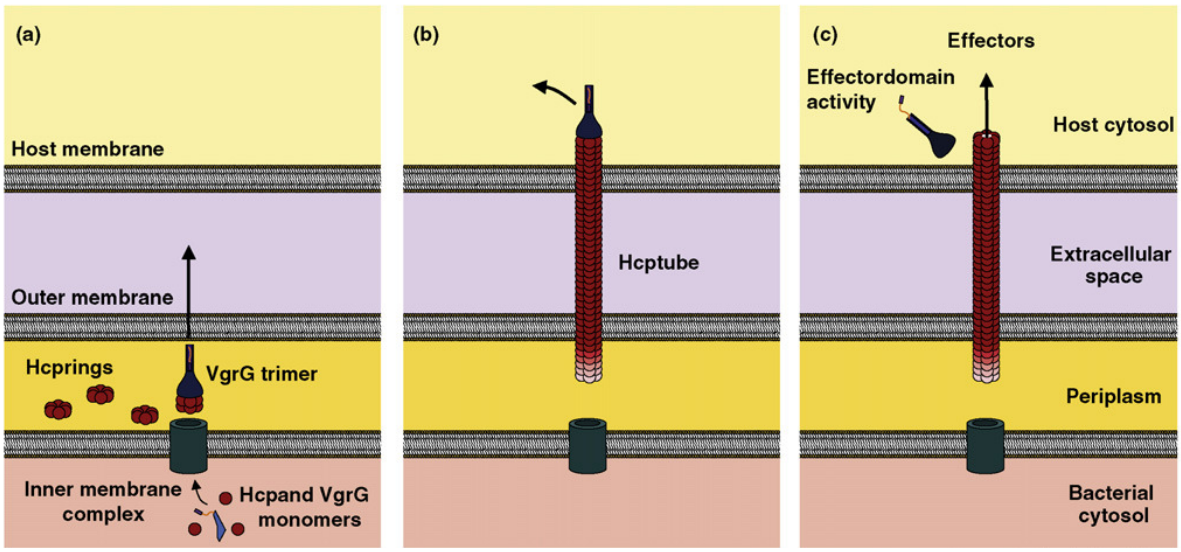


Schematic representation of the different secretion systems found in *E. amylovora*. In contrast to the direct protein translocation by the type I, type III, and type VI secretion systems from the cytoplasm to the extracellular medium, the proteins secreted by the type II secretion systems pathway are firstly exported to the periplasm before crossing the outer membrane. The type I and type II secretion sysrems are involved in secretion of proteases, pectinases, and cellulases. The Hrp-T3SS translocates the DspA/E effector which is essential for virulence and cell death induction on apple trees. (The figure is adapted for *E. amylovora* from Bleves et al. (2010)).

The VgrG protein might puncture host cell membranes and subsequently allow the secretion of effectors (Pukatzki et al., 2007). In other bacteria the T6SS is involved, e.g., in non-pathogenic functions in inter-bacterial communication, biofilm formation and environmental

stress response (Schwarz et al., 2010a). Additionally, secreted effectors have been shown to have toxic effects on other bacteria (Hood et al., 2010; Zheng et al., 2011). In human pathogenic bacteria, T6SS genes have been shown to be implicated in virulence activities (Mougous et al., 2006; Pukatzki et al., 2006; Zheng and Leung, 2007), whereas only a few reports exist about functions in plant-associated bacteria. In the plant symbiotic bacterium *Rhizobium leguminosarum* bv. *trifolii* the T6SS inhibited the ability to effectively nodulate pea and was thus named the *imp* locus (impaired in nodulation) (Roest et al., 1997).

Figure 3



Schematic representation of T6SS effectors delivery. (**a**) Hcp and VgrG monomers are exported into the periplasm through an inner membrane complex. In the periplasm, Hcp monomers hexamerize into rings that dock beneath spike-like VgrG trimer. (**b**) The assembly of further Hcp ring beneath VgrG creates an elongation tube that pushes through the outer membrane. Upon host membrane contact the pilus-like structure punctures it to (**c**) expose effector-domains of VgrG allowing it to interact with host target molecules and affect host cell function. If the VgrG is detached, it leaves a uncapped Hcp tube that facilitates the secretion of effector protein to the host cell. (Pukatzki et al., 2009)

Expression of T6SS genes was induced when *Agrobacterium tumefaciens* and *Pectobacterium atrosepticum* were grown under plant mimicking conditions (Mattinen et al., 2007; Yuan et al., 2008). Secretome analyses of both bacteria confirmed functionality of the T6SSs, but virulence assays gave differing results (Mattinen et al., 2007; Wu et al., 2008). While the deletion of a gene encoding for an effector protein Hcp resulted in a decreased virulence in *A. tumefaciens*, a mutant unable to secrete the effector Hcp in *P. atrosepticum* had increased

virulence. The T6SS have versatile functions and deletion mutants produce distinct phenotypes in different bacteria.

Pantoea vagans C9-1 – a biocontrol agent of *E. amylovora*

Pantoea vagans C9-1 is a registered biocontrol agent of *E. amylovora* in the USA and Canada (BlightBan C9-1, NuFarm Americas, Burr Ridge, IL). *Pantoea agglomerans* strains E325 and P10c are also commercially available for fire blight control (Bloomtime Biological, Northwest Agricultural Products, Pasco, WA) and Blossom Bless (Gro-Chem, AgriNova NZ Ltd, Porirua, NZ). The introduction of these biocontrol agents to the European market is constrained by the reporting of clinical strains, often not well documented and misidentified, within the same species (Rezzonico et al., 2012). This led to the classification of most *Pantoea* spp. as biosafety level 2 organisms (opportunistic pathogens) and restricts the beneficial uses needed to replace more controversial products (e.g., antibiotics). No evidence of potential phytopathogenic or animal virulence factors were found in the genome sequence of *P. vagans* C9-1 (Smits et al., 2011).

A primary control measure of *E. amylovora* is the application of antibiotics (e.g., streptomycin and oxytetracyline) during bloom to suppress epiphytic growth and subsequent infection. Emerging antibiotic resistance of the pathogen raises the need for further fire blight management measures (Loper et al., 1991). The application of biocontrol agents have been proven to significantly reduce fire blight disease incidence in field trials (Stockwell et al., 2010). Several modes of action of antagonists have been described. The competition for nutrients and space is one of the most common mechanisms (Wilson & Lindow, 1994). Acidification and antibiosis of biocontrol agents can effectively suppress the growth of the pathogen (Pusey et al., 2008, Stockwell et al., 2002, Vanneste et al., 1992). The production of one or multiple antibiotics effective against *E. amylovora* have been reported for many *Pantoea* species (Ishimaru et al., 1988; Wodzinski and Paulin, 1994; Stockwell et al., 2002) but the biosynthesis genes of only a few have been identified (Giddens et al., 2002; Jin et al., 2006). To improve the screen for novel antibiotic producing biocontrol agents the respective genes need to be identified. *P. vagans* C9-1 produces at least two antibiotics, pantocin A and herbicolin I inhibiting the growth of *E. amylovora* (Ishimaru et al., 1988). The pantocin A biosynthesis genes (Smits et al., 2011) and the chemical structure were identified previously (Jin et al., 2003), whereas such information for herbicolin I antibiotic was lacking. In order to fill this gap, the herbicolin I antibiotic and the biosynthesis genes were characterized and described in **Chapter 4**.

Malus x domestica – host plant of *E. amylovora*

The cultivated apple (*Malus* x *domestica* Borkh.) is one of the most important horticultural fruit crops worldwide. With other important fruit and ornamental plants, including pear (*Pyrus communis*), peach (*Prunus persica*), cherry (*Prunus avium*), strawberry *(Fragaria* spp.), apricot (*Prunus armeniaca*), almond (*Prunus amygdalus*) and *Sorbus* (*Sorbus* spp.) it belongs to the Rosaceae family. Fire blight affects primarily the subfamily Spiraeoideae of the Rosaceae including the genera *Malus*, *Pyrus*, *Cydonia* (quince), *Cotoneaster*, *Crataegus* (hawthorn), *Pyracantha* (firethorn) and *Sorbus* (e.g., rowan). This wide host range of *E. amylovora* and the limited number of management measures available makes it difficult to control or slow down the disease spread. Practices applied (beside the afore mentioned) include the use of fire blight resistant rootstocks and chemical enhancement of host resistance (Maxson-Stein et al., 2002; Norelli et al., 2003b). Genetically engineered apple with improved resistance to fire blight are promising, but have only a low commercial acceptance from customers (Malnoy et al., 2007). Classical apple breeding programs aim at high fruit quality, resistance to main disease (e.g., fire blight, scab, and powdery mildew), but due to the nature of *M.* x *domestica*, (e.g., self-incompatibility, for cultivars only clonal propagation on rootstocks possible, high heterozygosity, prenniality, and large plant size) breeding is a long term and labour-intensive approach. The most important apple cultivars currently produced are susceptible to fire blight (e.g., 'Golden Delicious', 'Gala'); therefore fundamental knowledge of the underlying processes is essential to develop novel control measures.

To gain insights into specific responses and underlying processes of apple to *E. amylovora*, transcriptome studies were performed in susceptible and resistant cultivars. These studies applied microarray, suppression subtractive cDNA hybridization or cDNA amplified fragment length polymorphism techniques (Norelli et al., 2009; Baldo et al., 2010; Sarowar et al., 2011). This gave first insights into the apple–fire blight interaction. The recent publication of the apple genome sequence (Velasco et al., 2010) enables transcriptome studies of the *E. amylovara* and *Malus* interaction in its genomic background. The analysis of transcriptomic data by RNA-sequencing (RNA-seq) in the genomic background is advantageous to other techniques relying on expressed sequence tags (EST) libraries, as these often contain partial sequences and probes designed might not cover all genes of a genome. Additionally, splice variants and homologous genes with minimal variation cannot be detected and might be misinterpreted. RNA-seq is based on high-throughput sequencing technologies (e.g., Illumina sequencing) to sequence cDNA derived from RNA samples in order to get information about

its content. The deep coverage and base-level resolution can be used to analyze differential gene expression, including alleles and splice variants, as well as post-transcriptional mutations or editing. RNA-seq was used to analyze the transcriptional changes of susceptible apple ('Golden Delicious') induced by *E. amylovora* (**Chapter 5**).

Objectives

The overall aim of this thesis was to elucidate and characterize factors potentially involved in *E. amylovora* virulence, the interaction of *E. amylovora* – with its host plant apple and the interaction of *E. amylovora* with the biocontrol agent *P. vagans* C9-1. Although many important virulence and fitness determinants have been identified, novel factors potentially contributing or modulating pathogenicity of *E. amylovora* can be discovered. The recent availability of genome sequences of the genus *Erwinia* enables comparative genomics studies that identify determinants like the type VI secretion systems of *E. amylovora*. These secretion systems have various functions in different bacteria, e.g., as important virulence factor, in bacterial communication, as anti-bacterial toxin delivery system, and affecting host-specificity. Given the versatility of this secretion system in other bacteria, the first aim of this thesis was to analyze the function and potential contribution of the T6SSs to the virulence of *E. amylovora*. Functionality of the systems were proven and thus plant assays and transcriptomic analysis performed.

A control measure to protect susceptible host plants from fire blight is the application of biocontrol agents during bloom. A main factor contributing to the efficacy of biocontol agents is the biosynthesis of antibiotics that inhibit the growth of *E. amylovora*. Characterization and identification of the corresponding genes can be used to screen for and assess novel biocontrol agents. Therefore, the second aim of this thesis was the characterization and identification of the antibiotic biosynthesis gene cluster for herbicolin I in *P. vagans* biocontrol strain C9-1.

The most important apple cultivars are susceptible to the fire blight disease. Thus fundamental knowledge of induced and repressed pathways/genes in this compatible interaction is needed to understand the underlying mechanisms and to develop novel control measures. Therefore, the third aim was to analyze the apple trancriptome of 'Golden Delicious' in response to *E. amylovora* using RNA-seq. Main transcriptional changes were identified and potential new genes could be assigned to the apple genome sequence.

Chapter 2

Genomics and current genetic understanding of *Erwinia amylovora* and the fire blight antagonist *Pantoea vagans*

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Genomics and current genetic understanding of *Erwinia amylovora* and the fire blight antagonist Pantoea vagans

Abstract

The bacterial plant pathogen *Erwinia amylovora* causes fire blight, a major disease threat to pome fruit production worldwide with further impact on a wide-range of *Rosaceae* species. Important factors contributing to the development of the disease were discovered in the last decades. Comparative genomics of the genera *Erwinia* and *Pantoea* is coming into focus with the recent availability of complete genome sequences. Insights from comparative genomics now position us to answer fundamental questions regarding the evolution of *E. amylovora* as a successful pathogen and the critical elements for biocontrol activity of *Pantoea* spp. This trove of new data promises to reveal novel determinants and to understand interactive pathways for virulence, host range and ecological fitness. The ultimate aim is now to apply genomics and identify the pathogen Achilles heels and antagonist mechanisms of action as targets for designing innovative control strategies for fire blight.

Introduction

The enterobacterium *Erwinia amylovora* is the causal agent of the fire blight disease, threatening global pome fruit production (i.e., apple, pear) and a wide-variety of *Rosaceae* (Spiraeoideae, Maloideae, *Rubus*) species, including ecological cornerstone species (e.g., forest, landscape and rural ecosystems). The pathogen first was described in the late 1790s and originated in North America. From there it has relatively recently dispersed to New Zealand in the late 1910s, the United Kingdom and Northern Europe in the late 1950s and the Middle East in the mid-1960s (Bonn and van der Zwet, 2000). Since the first reports of fire blight in Europe, the pathogen has continued to spread across the continent (Jock et al., 2002) and now threatens Central Asia, the germplasm region of origin for apple and pear. The quarantine status of *E. amylovora* in many countries imposes further economic losses from phytosanitary control measures and as a highly-charged trade (Calvin and Krissoff, 1998).

The general epidemiology of fire blight is well understood and is the basis for current control strategies. *E. amylovora* lacks enzymatic means for penetrating healthy host tissues and infects plants through natural openings (e.g., floral nectaries, leaf hydathodes) and via wounds (e.g., from hail or insect damage). Once inside a host, the pathogen can spread in the plant through the vascular system (Billing, 2011), and aggressive sanitation is key to

removing inoculum reservoirs (e.g., tree removal) and preventing further advance within infected hosts (e.g., pruning well beyond visible disease symptoms). Dependent on the infected plant part the disease develops as flower, shoot or rootstock blight. Typical symptoms are flower necrosis, fruit rot, shepherd's crook in shoots, bacterial ooze and cankers in woody tissue. The disease develops under defined weather conditions that enabled the deployment of fire blight forecast models. Pathogen establishment and rapid infection of flowers (i.e., blossom blight) is the main infection court and epidemic driver of fire blight and thus the primary focus for preventative disease control efforts.

Control options against blossom blight include antibiotic and biocontrol agent application during bloom to reduce the epiphytic population of *E. amylovora*. Resistance to streptomycin (Chiou and Jones, 1995), the most effective antibiotic against *E. amylovora*, and regulatory restriction on antibiotic use in plant agriculture (McManus et al. 2002) demands development of novel control measures with comparable efficacy. Natural epiphytic bacteria of the closely related species *Pantoea agglomerans* and *Pantoea vagans* have proven to be among the most reliable and effective antagonists of *E. amylovora* when applied during bloom-time (Stockwell et al., 2010). *P. agglomerans* strains have been isolated from various environments (e.g., soil, plant, water) (Gavini et al., 1989; Rezzonico et al., 2009), reflecting their potential to successfully compete with indigenous microbial populations. The growth inhibition induced by *P. agglomerans* strains might result from nutrient competition, active site exclusion and antibiotic production or the combination of these processes (Vanneste et al., 1992; Wodzinski et al., 1994; Kearns and Mahanty, 1998; Pusey et al., 2008).

Although important insights have been acquired regarding this important phytopathogenic bacterium (Table 1), much remains uncertain about the evolutionary genetics of *E. amylovora*. The recent sequencing of eight *Erwinia* genomes (i.e., 3 *E. amylovora*, 2 *Erwinia pyrifoliae*, *Erwinia* sp., *Erwinia billingiae* and *Erwinia tasmaniensis*) (Kube et al., 2008; Kube et al., 2010; Sebaihia et al., 2010; Smits et al., 2010c; Smits et al., 2010b; Park et al., 2011) and three genomes of the closely related genus *Pantoea* (i.e., *P. vagans*, *P. agglomerans* and *Pantoea ananatis*) (De Maayer et al., 2010; Smits et al., 2010d) provides a solid genomics foundation to infer the species evolution within these genera.

Erwinia amylovora genomics

The genome of the *Crataegus* isolate *E. amylovora* CFBP 1430 was sequenced, consisting of a 3.8 Mb chromosome and the 28 kb plasmid pEA29 (Smits et al., 2010b). In total, 3736 CDS were automatically assigned using GenDB (Meyer et al., 2003) and manually curated. The

annotated genome allowed the identification of known virulence factor genes (e.g., *hrp* (hypersensitivity response and pathogenicity), amylovoran biosynthesis gene cluster) of *E. amylovora* in the genome (Oh and Beer, 2005), but also included the genes encoding several new putative factors, like two additional Inv/Spa-type type III secretion systems (T3SSs), a second flagellum and the complete desferrioxamine E biosynthesis cluster (Table 1) (Smits et al., 2010b).

Currently, two further *E. amylovora* genome sequences are available: *Malus* isolate Ea273 (ATCC 49946) and the *Rubus* isolate ATCC BAA-2158 (Powney et al., 2011). Comparison of the Ea273 genome to that of CFBP 1430 clearly shows that two large rearrangements must have occurred within the rRNA regions (Fig. 1) (Smits et al., 2010b) that could explain differences in the PFGE patterns observed before (Zhang and Geider, 1997; Jock et al., 2002). Several other, relatively small differences mainly in the ITS regions rendered the chromosome of Ea273 in total 301 bp larger than that of CFBP 1430. Nevertheless, the both genomes share over 99.99% sequence identity over the complete length, indicating only minimal evolution since the geographical dispersal. Plasmid pEA72, identified in the genome of *E. amylovora* Ea273 (Sebaihia et al., 2010), is absent in *E. amylovora* CFBP 1430.

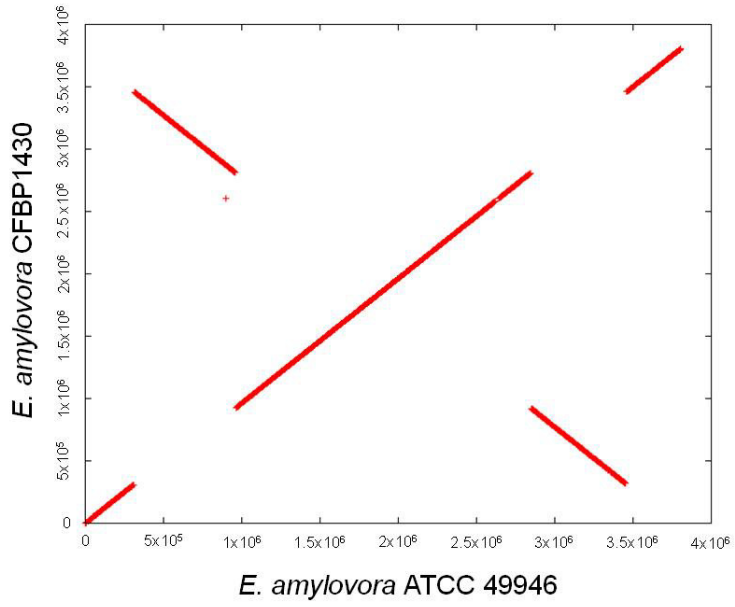

Figure 1 Synteny plot of *E. amylovora* strains CFBP 1430 and ATCC 49946 generated using EDGAR (Blom et al., 2009). The position of each CDS given on the X axis is plotted against the position of its ortholog in the other chromosome given on the Y axis. Identical gene organization on the chromosomes results in a diagonal plot, inversions and chromosomal rearrangements are plotted perpendicular to it.

The draft genome of the closely related but genetically distinct *E. amylovora* strain ATCC BAA-2158 with restricted pathogenicity to *Rubus* spp. was recently published (Powney et al., 2011). Also here, collinearity was obtained over large regions of the chromosome. This strain carries, in addition to pEA29, two small plasmids (pEAR4.3, pEAR5.2) (Table 2). A total of 373 singletons in this strain may give indications towards the restricted host range of this strain (Powney et al., 2011).

An obvious difference between the currently sequenced *E. amylovora* genomes is the presence of (cryptic) plasmids (Sebaihia et al., 2010; Smits et al., 2010b; Powney et al., 2011). Plasmids appear to be a major factor influencing the pan-genome of *E. amylovora.* However, although several plasmids of different sizes have been detected in isolates of this species (Laurent et al., 1989; Steinberger et al., 1990; Chiou and Jones, 1991; McGhee et al., 2002; Foster et al., 2004) , the knowledge on this extra-chromosomal material is limited to few strains and plasmids.

Erwinia inter-species genomics

Another five *Erwinia* genomes were recently sequenced, namely two *E. pyrifoliae* strains (DSM 12163^T and Ep1/96) (Kube et al., 2010; Smits et al., 2010c), *Erwinia* sp. Ejp617 (Park et al., 2011), *E. tasmaniensis* Et1/99 (Kube et al., 2008) and *E. billingiae* Eb661 (Kube et al., 2010) and are available for inter-species comparisons.

E. pyrifoliae, a close relative of *E. amylovora,* is primarily a pathogen of Asian or Nashi pear (*Pyrus pyrifolia*) with a restricted geographical distribution to East Asia (Kim et al., 1999). Disease symptoms caused by *E. pyrifoliae* are almost indistinguishable to those of *E. amylovora* (Rhim et al., 1999). Another pathogenic *Erwinia* species, causing bacterial shoot blight of pear in Japan, was first described as *E. amylovora* due to similar disease symptoms and was later found to be closer related to *E. pyrifoliae* than to *E. amylovora* (Mizuno et al., 2000; Matsuura et al., 2007; Geider et al., 2009). *E. tasmaniensis* strains were isolated from apple and pear as non-pathogenic epiphytic bacteria (Geider et al., 2006; Powney et al., 2011). The non-pathogenic *E. billingiae* was isolated as non-pigmented *E. herbicola* and later reclassified (Billing and Baker, 1963; Mergaert et al., 1999). Chromosomal collinearity of *E. amylovora* to the closely related *E. pyrifoliae* strains, *Erwinia* sp. Ejp617 and *E. tasmaniensis* was observed, but chromosomal large-scale rearrangements were detected. These ecologically distinct species harbor distinct plasmids with low sequence similarity. The genome sizes of the above described *Erwinia* species range from approximately 3.8 Mb to 4 Mb with the exception of *E. billingiae* having a genome size of 5.4

Mb (Table 2). The genome sizes of the sequenced pathogenic *Erwinia* spp. are markedly smaller compared to other enterobacterial genomes, likely the effect of genome erosion (Georgiades and Raoult, 2011). The loss of epiphytic fitness factors due to genome size reduction and the acquisition of the Hrp-type T3SS and genes needed for the biosynthesis of the exopolysaccharides levan and amylovoran are potentially a result of adaption to the pathogenic lifestyle.

Differential gene content can be displayed in Venn diagrams, calculated by reciprocal BLAST of all CDS to all the input sequences. Areas displayed in such a Venn diagram represent a subset of the compared genomes and the number of genes is indicated by numbers. The core genome (Tettelin et al., 2005) consists of CDS shared by all genome sequences, which usually includes metabolic and cellular functions. CDS shared by two or several species are present in overlapping regions. Areas not shared by any other pool of CDS (singletons) include accessory genes which may provide additional functions (virulence factors, host-range determinants, metabolic processes) and contribute to species variability (Blom et al., 2009).

The core genome of *E. amylovora* strain CFBP 1430, *E. tasmaniensis* Et1/99, *E. pyrifoliae* DSM 12163^T and the non-pathogenic *E. billingiae* Eb661 displays 2414 genes shared between these species. The genes only shared by *E. amylovora* CFBP 1430, *E. tasmaniensis* Et1/99 and *E. pyrifoliae* DSM 12163^T, in different combinations, include the most important virulence factors, e.g., T3SSs and the exopolysaccharides amylovoran and levan (Table 3). These genes are absent in *E. billingiae* Eb661 and might therefore represent the “pathogenic core” of disease eliciting *Erwinia* species (Fig. 2A). Virulence determinants setting host-range and specificity are most likely included in the singletons for the broad host range *E. amylovora*, and absent in the genomes of *Erwinia* species with restricted host-ranges (Fig. 2A).

Table 1 Genes and gene clusters assessed on potential impact on pathogenicity

	Gene(s)	Impact on pathogenicity	Assessment	Reference	Locus tag [a]
Type 1 secretion system	*prtADEF*	No	Immature pear fruits, apple seedlings	(Zhang et al., 1999)	EAMY_3577- 3581
Type 2 secretion system	*outCDEFFHJKLMNOS-chiV*	No	Immature pear fruits, apple seedlings	(Zhao et al., 2009)	EAMY_2865- 2878
Type 3 secretion system	*hrpN*	Yes	Immature pear fruits, no HR in tobacco leaves	(Wei et al., 1992)	EAMY_0552
	dspA/E	Yes	Immature pear fruits, apple and cotoneaster shoot	(Bogdanove et al., 1998)	EAMY_0557
	hrpW	No	Immature pear fruits and apple and pear seedlings	(Kim and Beer, 1998)	EAMY_0556
	hrpK	No	Immature pear fruits, apple shoots, HR tobacco plants	(Oh et al., 2005)	EAMY_0519
	hrpA	Yes	Apple seedlings, no HR tobacco leaves	(Jin et al., 2001)	EAMY_0542
	hrpJ	Yes	Immature pear fruits , reduced HR tobacco leaves	(Nissinen et al., 2007)	EAMY_0535
	orfB (*eopB, eop1*)	No	Immature pear fruit assay	(Asselin et al., 2006)	EAMY_0554
Additional T3SS effectors	*eop2* (*hopAK1*)	?		(Nissinen et al., 2007)	EAMY_0653
	eop3	?		(Nissinen et al., 2007)	EAMY_2270

	hopPtoC	No	Immature pear	(Zhao et al., 2005)	EAMY_0744
	avrRpt2	Reduced	Immature pear	(Zhao et al., 2006)	EAMY_3175
Chaperones	*dspB/F*	Reduced	Pear seedlings	(Gaudriault et al., 2002)	EAMY_0558
	orfA	No	Immature pear fruits	(Asselin et al., 2006)	EAMY_0553
T3SS associated	*hsvABC*	Yes apple/ no pear	Immature pear fruits, apple shoots, HR in tobacco	(Oh et al., 2005)	EAMY_0520- 0522
Regulators	*hrpY*	Yes	Immature pear fruits, no HR in tobacco	(Wei et al., 2000)	EAMY_0538
	hrpX	Reduced	Immature pear fruits, no HR in tobacco	(Wei et al., 2000)	EAMY_0537
	hrpS	Yes	Immature pear fruits, no HR in tobacco	(Wei and Beer, 1993)	EAMY_0539
	hrpL	Yes	Immature pear fruits, no HR in tobacco	(Wei and Beer, 1995)	EAMY_0536
Inv/Spa-type	PAI-2	No	Immature pear fruits/apple seedlings	(Zhao et al., 2009)	EAMY_0771- 0792
	PAI-3	No	Immature pear fruits/apple seedlings	(Zhao et al., 2009)	EAMY_1573- 1593
Iron uptake, siderophores	*dfoJAC*	Yes flowers/ no shoots	Apple seedlings/apple flower	(Dellagi et al., 1998)	EAMY_3238- 3240
	foxR	Yes	Apple seedlings/apple flower	(Dellagi et al., 1998)	EAMY_3241

Metabolism					
Sorbitol	*srlAEBDMR*	Yes apple/ no pear	Immature pear/apple shoots	(Aldridge et al., 1997)	EAMY_3071- 3076
Exopolysaccharide					
Levansucrase	*lsc*	Reduced	Pear seedlings	(Geier and Geider, 1993)	EAMY_3695
Amylovoran	*amsABCDEFGHI*	Yes	Pear slices/pear seedlings	(Bellemann and Geider, 1992)	EAMY_2241-2253
Regulator	*rscBCD*	Yes	Immature pear fruits	(Wang et al., 2009a)	EAMY_2342-2343

[a] Locus tags derive from *E. amylovora* CFBP 1430 (accession number FN434113)

Selected features clarified using comparative genomics

Type III secretion systems

T3SSs are part of the "pathogenic core" and are absent in *E. billingiae* Eb661. The Hrp T3SS genes were identified in *E. pyrifoliae* DSM 12163^T (Smits et al., 2010c) and *E. tasmaniensis* Et1/99 (Kube et al., 2008) showing differences in gene content compared to *E. amylovora* CFBP 1430 (Smits et al., 2010b). *E. tasmaniensis* Et1/99 lacks the HAE region present in the other two species, as well as ORFU1 and ORFU2 that are only present in *E. amylovora* CFBP 1430 (Fig. 3A). Proteins of *E. amylovora* secreted by the Hrp-T3SS have been demonstrated to be essential for pathogenicity on host plants (Table 1) (Oh and Beer, 2005). The Hrp T3SS gene cluster is located on pathogenicity island 1 (PAI-1) and consists of the *hrp/hrc* region, flanked by the Hrp effectors and elicitors (HEE) region and the Hrp-associated enzymes (HAE) region. The Hrp/Hrc region contains regulatory genes as well as genes encoding for secreted proteins.

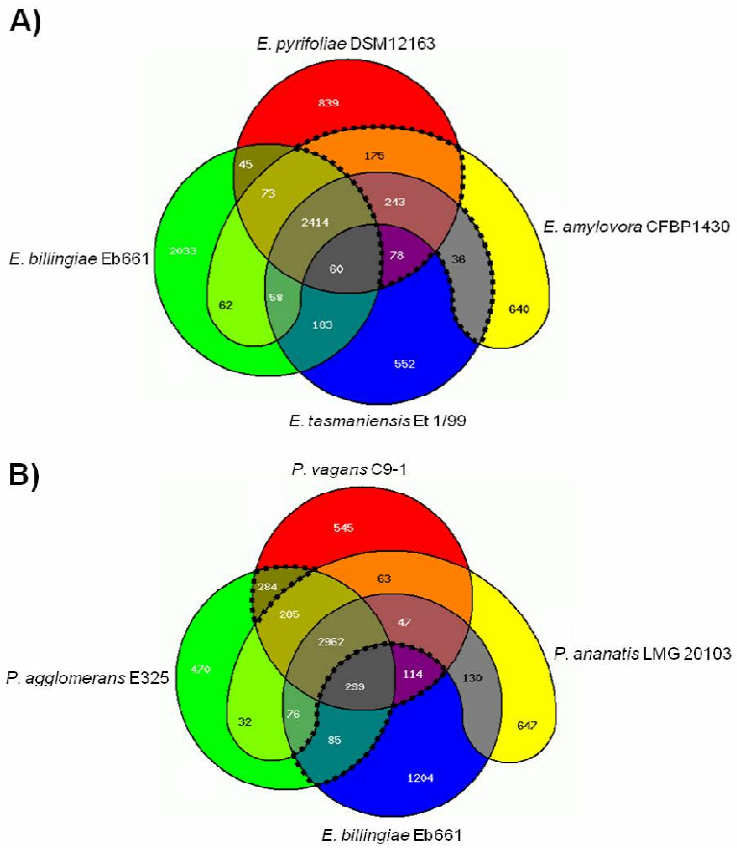

Figure 2 Venn diagram of *Erwinia* spp. (A) and *Pantoea* spp. including *E. billingiae* (B) generated using EDGAR. The numbers of CDS is indicated. Overlapping areas indicate shared CDS. The "pathogenic" (Fig. 2A) - and "biocontrol" core (Fig. 2B), respectively, are indicated by dotted lines.

Table 2 Summary of sequenced genomes of *Erwinia* and *Pantoea*

Species/Strain	Host/origin	Status	Genome	Size (Mb)	CDS	Reference
E. amylovora CFBP 1430	*Crataegus sp.* (Hawthorn), France	Finished	Chromosome	3.806	3706	(Smits et al., 2010b)
			pEA29	0.028	28	
E. amylovora ATCC 49946	*Malus x domestica* (Apple), USA	Finished	Chromosome	3.806	3483	(Sebaihia et al., 2010)
			pEA72	0.071	87	
			pEA29	0.028	28	
E. amylovora ATCC BAA-2158	*Rubus* sp. (Blackberry), USA	Draft	Chromosome (29 contigs)	3.81	3831	(Powney et al., 2011)
			pEA29	0.028	28	
			pEAR5.2	0.005	6	
			pEAR4.3	0.004	4	
E. pyrifoliae DSM 12163^T	*Pyrus pyrifolia* (Asian pear, Nashi), South Korea	Finished	Chromosome	4.026	3986	(Smits et al., 2010c)
			pEP36	0.036	40	
			pEP5	0.005	7	
			pEP3	0.003	4	
			pEP2.6	0.003	1	
E. pyrifoliae Ep1/96	*Pyrus pyrifolia* (Asian pear, Nashi), South Korea	Finished	Chromosome	4.026	3645	(Kube et al., 2010)
			pEP36	0.036	37	
			pEP5	0.005	5	
			pEP3	0.003	4	
			pEP2.6	0.003	6	

Erwinia sp. Ejp617	*Pyrus pyrifolia* (Asian pear, Nashi), Japan	Finished	Chromosome	3.909	3600	(Park et al., 2011)
			pEJP30.8	0.031	34	
			pEJP6.4	0.006	0	
			pEJP5.2	0.005	6	
			pEJP3.2	0.003	0	
			pEJP2.6	0.003	0	
E. tasmaniensis Et1/99	*M. x domestica* (Apple), Australia	Finished	Chromosome	3.883	3427	(Kube et al., 2008)
			pET49	0.049	61	
			pET46	0.046	39	
			pET45	0.045	46	
			pET35	0.035	42	
			pET09	0.009	7	
E. billingiae Eb661	*P. communis* (Pear) UK	Finished	Chromosome	5.1	4587	(Kube et al., 2010)
			pEB170	0.17	220	
			pEB102	0.102	114	
P. vagans C9-1	*M. x domestica* (Apple), USA	Finished	Chromosome	4.025	3665	(Smits et al., 2010d)
			pPag1	0.168	162	
			pPag2	0.166	229	
			pPag3	0.53	535	
P. agglomerans E325	*M. x domestica* (Apple), USA	Draft	Genome	4.774	4495	(Smits & Duffy, unpublished)
P. ananatis LMG 20103	*Eucalyptus grandis* x *E. nitens* hybrid A. (Eucalyptus), South Africa	Finished	Chromosome	4.69	4272	(De Maayer et al., 2010)

DspA/E and HrpN encoded by genes in the HEE are secreted proteins essential pathogenicity factors of *E. amylovora* (Wei et al., 1992; Gaudriault et al., 1997). The products of the hrp-associated systemic virulence genes (*hsv*) encoded in the HAE region are required for systemic infection of host plants (Oh et al., 2005).

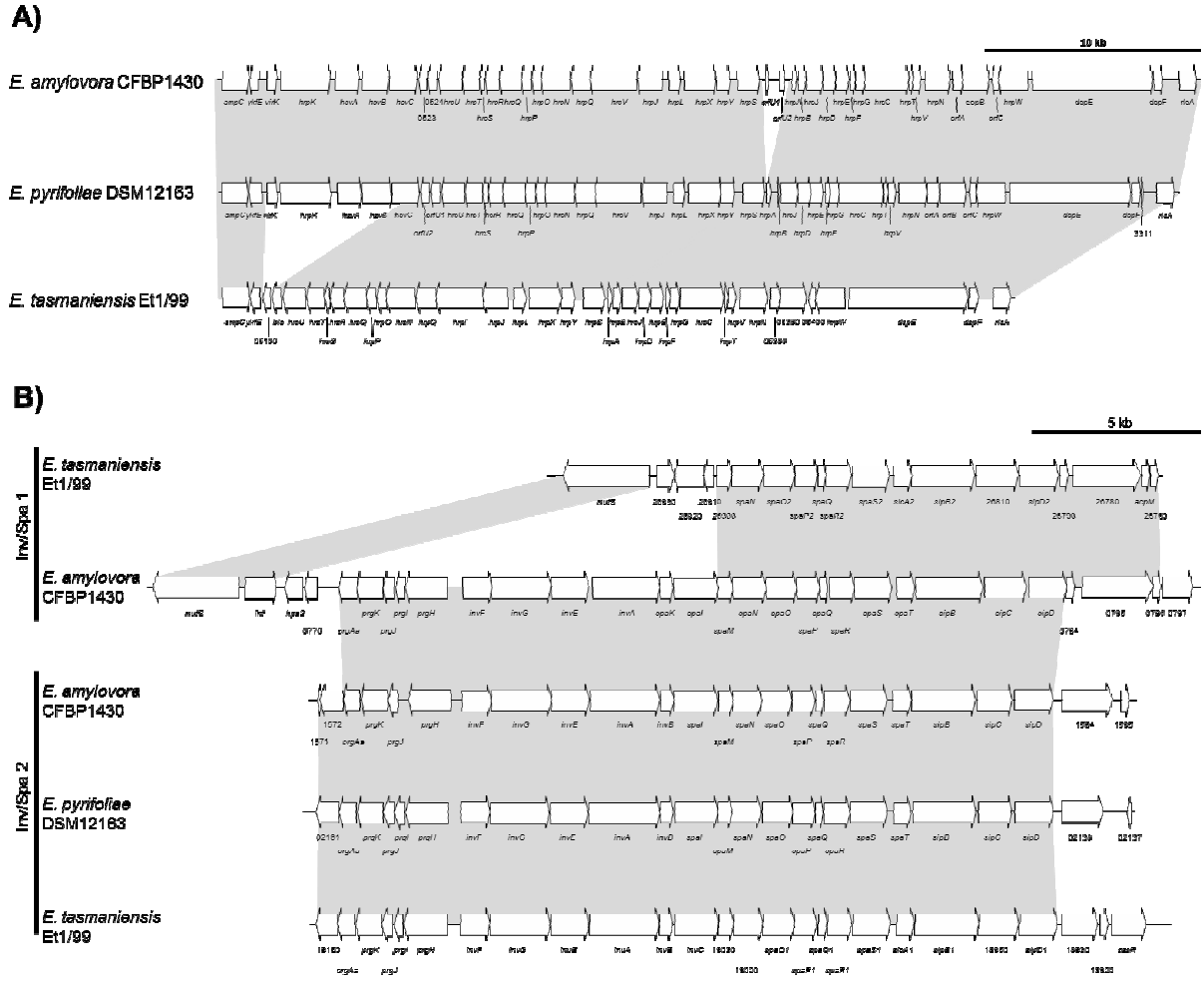

Figure 3 Comparison of the Hrp (A) and Inv/Spa-type (B) Type III Secretion Systems in *E. amylovora* CFBP 1430, *E. pyrifoliae* DSM 12163^T and *E. tasmaniensis* Et1/99. Related genes are shaded grey.

Additional T3SSs (Inv/Spa-1, Inv/Spa-2) were identified in the genomes of the pathogenic *Erwinia* spp. that differ in gene content. While the *inv/spa-2* gene cluster is present in *E. amylovora* CFBP 1430, *E. pyrifoliae* DSM 12163^T and *E. tasmaniensis* Et1/99, the *inv/spa-1* gene cluster is absent in *E. pyrifoliae* DSM 12163^T and only partially present in *E. tasmaniensis* Et1/99 (Fig. 3B). The *inv/spa*-type T3SSs are located in low G+C regions on the chromosome of the three *Erwinia* spp. and might therefore be an acquired trait. The *inv/spa*-type T3SSs are similar to the *Salmonella* pathogenicity island SPI1 T3SS of *Salmonella typhimurium* LT-2 (McClelland et al., 2001) and the *inv/spa* T3SS of the insect endosymbiont

Sodalis glossinidius (Dale et al., 2001) and are not directly implicated in virulence on host plants (Zhao et al., 2009).

Exopolysaccharides

The *E. amylovora* CFBP 1430 and *E. pyrifoliae* DSM 12163^T exopolysccharide gene clusters differ from the respective clusters in *E. tasmaniensis* Et1/99 and *E. billingiae* Eb661 by an exchange of two glycosyltransferases (Fig. 4) resulting potentially in the production of amylovoran. Amylovoran biosynthesis is a specific virulence factor in *E. amylovora* and *E. pyrifoliae* reflected in the fact that deletion or mutagenesis of specific genes renders the pathogens avirulent (Bellemann and Geider, 1992; Kim et al., 2002). The exopolysaccharide gene clusters, producing CPS of the two non-amylovoran producing species and also of *Pantoea* spp., might represent the ancestral state.

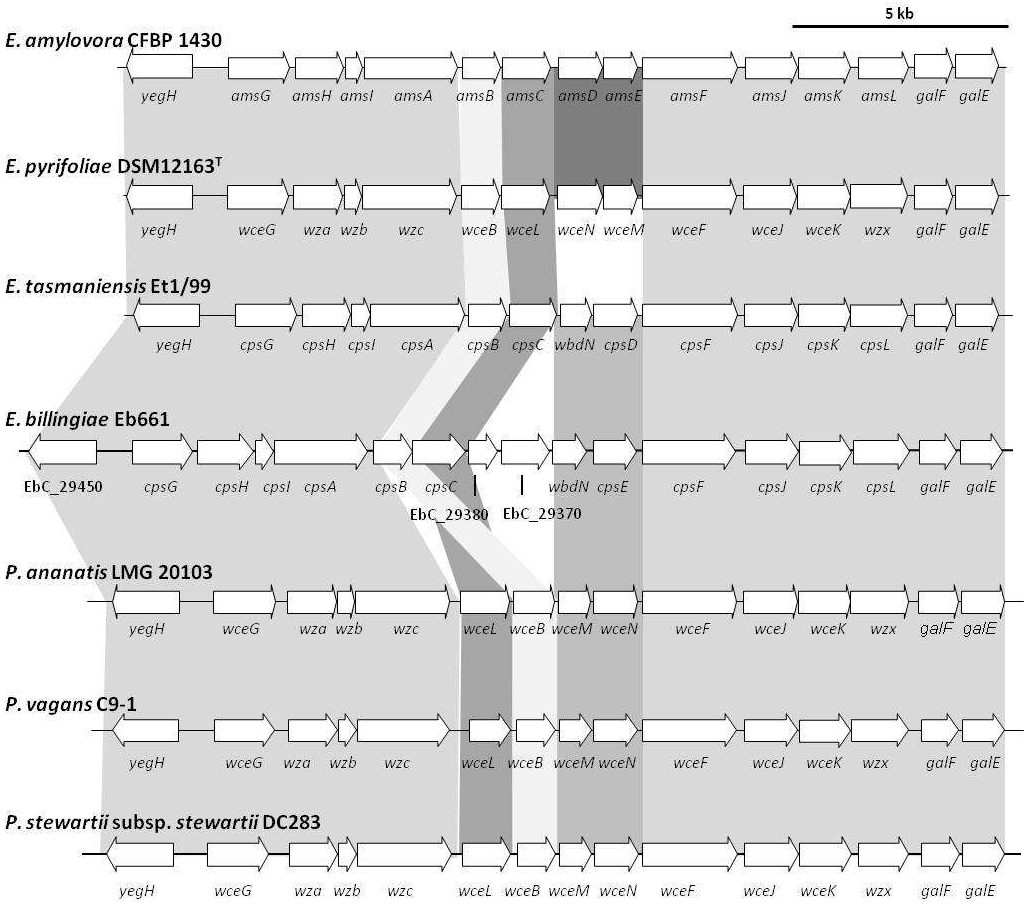

Figure 4 Comparison of the exopolysaccharide gene clusters of *Erwinia* spp. and *Pantoea* spp. Related genes are shaded.

Table 3 Selected factors analyzed by comparative genomic approaches. Presence or absence of genes and gene cluster are indicated by the symbols + and –, respectively.

Species (Strain)	T3SS			Exopolysaccharides			Flagellar		Siderophores			Sorbitol
	Hrp	Inv/ Spa-1	Inv/ Spa-2	AMS	CPS	*lsc*	Flg1	Flg2	*foxR/A*	*dfoJAC*	Ent	Srl
E. amylovora (CFBP 1430, ATCC 49946)	+	+	+	+	-	+	+	+	+	+	-	+
E. pyrifoliae (DSM 12163^{T}, Ep1/96)	+	-	+	+	-	-	+	+	+	+	-	+
Erwinia sp. (Ejp617)	+	-	+	+	-	-	+	+	+	+	-	+
E. tasmaniensis (Et1/99)	+[a]	+[b]	+	-	+	+	+	-	+	+	-	-
E. billingiae (Eb661)	-	-	-	-	+	-	+	-	+	+	-	+
P. vagans (C9-1)	-	-	-	-	+	-	+	-	+	+	+	+
P. agglomerans (E325)	-	-	-	-	+	-	+	-	+	+	+	-
P. ananatis (LMG 20103)	-	-	-	-	+	-	+	-	+	+	-	+

[a] HAE absent

[b] Partial

The additional exopolysaccharide levan is only produced by *E. amylovora* and *E. tasmaniensis,* whereas not by *E. billingiae* and *E. pyrifoliae*. The gene encoding the levansucrase, responsible for the synthesis of levan, most likely was acquired by a common ancestor of *E. amylovora, E. tasmaniensis* and *E. pyrifoliae*. The gene is retained by *E. amylovora* and *E. tasmaniensis,* whereas lost by *E. pyrifoliae*.

Siderophores

All up to now sequenced genomes of *Erwinia* spp. contain the desferrioxamine E siderophore biosynthesis gene cluster (Kube et al., 2010; Smits et al., 2010c; Smits et al., 2010b), whereas the enterobactin gene cluster, producing the catecholate siderophore enterobactin found in the genomes of many enterobacteria is absent.

Iron is an essential nutritional factor, required as cofactor for many proteins. In iron deprived environments high-affinity iron uptake siderophores are secreted to the environment to gain access to this limited factor by removing it from minerals and organic substances. *Erwinia* spp. produce the hydroxamate siderophore desferrioxamine E (Feistner et al., 1993; Kachadourian et al., 1996) and the specific TonB-dependent ferrioxamine receptor FoxR, both involved in iron uptake. Mutation of these genes leads to colonization defects of *E. amylovora* on flowers (Dellagi et al., 1998), whereas DFO E might be protective to oxidative conditions (Venisse et al., 2003).

Phylogenomic applications

A core genome tree was constructed (Fig. 5) which displays the phylogeny of the genus *Erwinia* which is in accordance to trees based on *gyrB* sequences. On both trees, *E. billingiae* groups to the *Erwinia* spp. and is the most distantly related *Erwinia* species sequenced until now. The position of *E. billingiae* seems to be close to the genus delineation between *Erwinia* and *Pantoea*. The marked difference in genome size, approximately 5.4 Mb *E. billingiae* Eb661 versus the nearly 4 Mb for the other *Erwinia* spp., might be the result of genome size reduction during specification to plant pathogenicity in the latter species. The Hrp, Inv/Spa-1, Inv/Spa- 2 T3SSs, absent in the genome of *E. billingiae*, might have been acquired by the pathogenic *Erwinia* ancestor, prior the divergence of *E. amylovora, E. pyrifoliae* and *E. tasmaniensis*.

Erwinia billingiae

The genera *Erwinia* and *Pantoea* are closely related (Hauben et al., 1998), which is supported by the core genome tree (Fig. 5) and the fact that gene synteny across the genus border is retained for large regions. *E. billingiae* first was isolated and described as non-pigmented *E. herbicola* (Billing and Baker, 1963) (now *P. agglomerans* (Gavini et al., 1989)) and later reassigned to *E. billingiae* (Mergaert et al., 1999).

The exopolysaccharides amylovoran and levan are not produced by *E. billingiae,* but a capsular polysaccharide (CPS) similar to that of *Pantoea* spp. is formed. Compared to *Pantoea* spp., the CPS gene cluster in *E. billingiae* Eb661 has an inversion of two genes that is distinct for the members of the genus *Erwinia*. The number of CDS shared by other *Erwinia* species and *E. billingiae* (Fig. 2A) in the core genome is smaller (approximately 500 CDS) than the core genome calculated when *E. billingiae* is included with *Pantoea* species (Fig. 2B). The genes shared with *Pantoea* include many carbohydrate uptake and utilization pathways and phosphonate utilization; genes absent in other *Erwinia* spp. These genes, possibly involved in the epiphytic fitness, were lost in the course of genome size reduction towards a more specific plant-associated or pathogenic lifestyle.

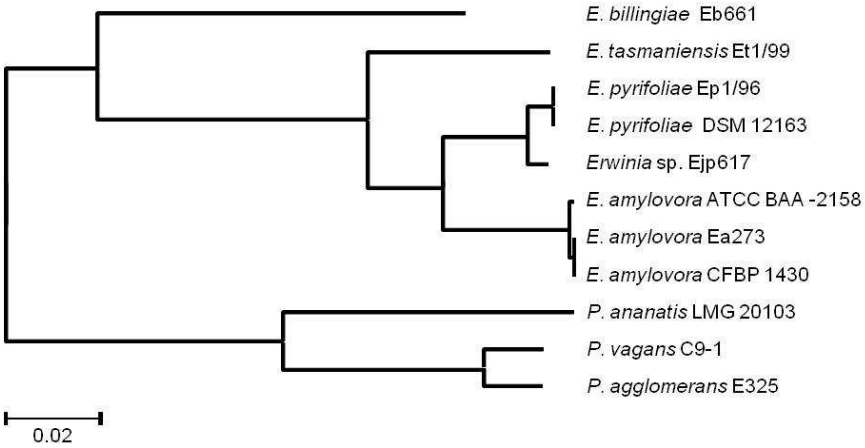

Figure 5 Phylogenetic tree based on the 2022 core genes of *Erwinia* and *Pantoea* spp. generated using EDGAR. Percent divergence is indicated by the scale bar.

Pantoea biocontrol agent genomics

The genome of the biocontrol agent *P. vagans* C9-1 (Ishimaru et al., 1988; Rezzonico et al., 2009; Rezzonico et al., 2010) was recently sequenced, consisting of a 4,025 Mb circular chromosome and the three plasmids pPag1, pPag2 and pPag3 (Smits et al., 2010d). A total of

4,619 CDS were assigned using GenDB (Meyer et al., 2003) and manually annotated. Genome sequencing of *P. agglomerans* E325 (Pusey, 1997; Pusey et al., 2008), a second biocontrol agent, is in progress (Smits & Duffy, unpublished). The genome sequences of both *Pantoea* spp. lack known enterobacterial virulence determinants such as T3SSs, toxins and pectolytic enzymes. A large repertoire of carbohydrate metabolic pathways, epiphytic fitness genes (e.g., AI-1 quorum sensing genes, IAA and carotenoid biosynthesis) and the biosynthetic genes for the antibacterial metabolite pantocin A were identified in the genome sequence of *P. vagans* C9-1 (Smits et al., 2010d).

Pantoea comparative genomics

Additional to the two biocontrol strains, the genome of *P. ananatis* LMG 20103, the causative agent of *Eucalyptus* blight and dieback, was sequenced (De Maayer et al., 2010) and was therefore included in comparative genomics analysis. Although being described as a plant pathogen (Goszczynska et al., 2006; Goszczynska et al., 2007), its genome sequence lacks T3SSs, a major virulence factor in many plant-associated pathogens, rendering this organism an unusual plant pathogen (Coutinho and Venter, 2009).

The calculated core genome of *P. ananatis* LMG 20103, *P. vagans* C9-1, *P. agglomerans* E325 and *E. billingiae* Eb661 (Fig. 2B) includes, additionally to the genes of the *Erwinia* core genome, carbohydrate metabolic pathways for maltose, rhamnose, glucarate, xylose, uronate, L-lactate, acetate as well as utilization of phosphonates, and many transporters (all types). Genes absent in the genome of the plant pathogen *P. ananatis* LMG 20103, but shared by the two other *Pantoea* and/or *E. billingiae* might represent the "biocontrol core" (Fig. 2B) due to the fact that genes potentially contributing to epiphytic fitness (e.g., nitrate assimilation, enterobactin synthesis genes) are common to these groups. Other factors implied in biocontrol efficacy, such as antibiotic biosynthesis, are not shared between the *Pantoea* spp. since they produce different antibiotics (Ishimaru et al., 1988; Pusey et al., 2008; Coutinho and Venter, 2009). The antibiotic pantocin A biosynthesis genes, for example are only present in *P. vagans* C9-1, whereas absent in *P. ananatis* LMG 20103, *P. agglomerans* E325 and *E. billingiae* Eb661. The biosynthesis genes of *P. vagans* C9-1 are located on a low-G+C genomic island of about 29 kb, which was probably acquired by horizontal gene transfer (Smits et al., 2010d; Smits et al., 2010a). The exopolysaccharide gene clusters of the *Pantoea* spp. are similar, whereas the *E. billingiae* cluster differs by inversion of two genes (Fig. 4).

Perspectives

The available sequenced *Erwinia* genomes from different hosts enable the identification of virulence, host-specificity and metabolic determinants involved in pathogenicity by comparative genomic analysis. The analyses could yield the information needed to develop novel control measures for the fire blight disease. Genome sequencing and analysis of *Pantoea* spp. will reveal their potential, and for the already successfully used as biocontrol agents, uncover the factors (metabolism, antibiotic production) responsible for effective biocontrol. As more *Erwinia* and *Pantoea* genomes get sequenced, these can be used to consolidate the current data as well as refine evolutionary aspects.

Acknowledgements

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Chapter 3

Identification of the type VI secretion regulome in *Erwinia amylovora* using RNA-seq

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Identification of the type VI secretion regulome in *Erwinia amylovora* using RNA-seq

Abstract

Type VI secretion systems (T6SS) were recently discovered to be apparently widespread among Gram-negative bacteria as essential virulence factors or to maintain symbiotic interaction. We recently identified three T6SS gene clusters in the genome of *E. amylovora* CFBP 1430. T6SS-C1 (27 genes) and T6SS-C3 (31 genes) include core genes of the T6SS machinery, whereas T6SS-C2 counts four genes only. To assess the contribution of T6SSs to virulence and potential transcriptomic changes of *E. amylovora* CFBP 1430, single and double mutants in two structural genes (*duf770*, *duf877*) were generated for T6SS-C1 and T6SS-C3 (ΔT6SS-C1, ΔT6SS-C3, ΔT6SS-C1C3). Plant assays showed that the ΔT6SS-C3 and ΔT6SS-C1C3 were more virulent in apple shoots and ΔT6SS-C1C3 less on apple flowers compared to the wild type (WT) strain. Nevertheless, the increase and decrease of symptoms were not pronounced and therefore T6SSs considered to have only a minor effect on virulence of *E. amylovora* CFBP 1430. RNA-sequencing was applied to obtain the transcriptomes of the WT and ΔT6SS-C1C3 from *in vitro* and *in planta* experiments. The mutations led under *in vitro* conditions to the differential expression of type III secretion systems, iron acquisition, chemotaxis, flagellar and fimbria genes. Comparison of the *in planta* and *in vitro* transcriptome data sets revealed these chemotaxis and motility genes were commonly differential in both data sets. Further experiments showed that T6SS mutants are impaired in their motility. These results suggest that the T6SSs influences metabolic and motility/chemotactic processes rather than being a virulence factor of *E. amylovora* CFBP 1430.

Introduction

Type VI secretion systems (T6SS) were discovered in ecologically-diverse pathogenic and non-pathogenic Gram-negative bacteria, including bacteria associated with eukaryotic cells maintaining pathogenic or symbiotic interaction (Records, 2011). T6SS gene clusters characteristically consists of a set of 13 core genes and a varying number of accessory genes (Boyer et al., 2009). These secretion systems are implied in various functions in different bacterial species, e.g., biofilm formation, interbacterial pathogenicity, host-cell invasion and survival within macrophages (Burtnick et al., 2010; de Pace et al., 2010; MacIntyre et al.,

2010; Schwarz et al., 2010b). The contribution of T6SS to virulence was demonstrated for certain animal and human pathogens (Schell et al., 2007; Blondel et al., 2010; Burtnick et al., 2010; Ma and Mekalanos, 2010) whereas only few reports about functions in plant associated bacteria exist (Mattinen et al., 2008; Haapalainen et al., 2012). In *Rhizobium leguminosarum*, the T6SS was first described as "*imp*" (impaired in nodulation) locus which negatively affects pea nodulation (Roest et al., 1997) and later identified as a secretion system (Bladergroen et al., 2003). A hallmark of functional T6SS is the secretion of the two core proteins, Hcp and VgrG that were identified in culture supernatants (Pukatzki et al., 2006; Mattinen et al., 2007; Wu et al., 2008). Microarray profiling and secretome analysis identified T6SS genes and proteins as putative virulence factors in *Pectobacterium atrosepticum* SCRI1043 (Mattinen et al., 2007; Mattinen et al., 2008) and *Agrobacterium tumefaciens* C58 (Wu et al., 2008). The putative effector genes *vgrG* and *hcp* in *P. atrosepticum* SCRI1043 were induced in the presence of plant extracts suggesting a potential role in virulence (Mattinen et al., 2008).

Erwinia amylovora is a Gram-negative enterobacterial phytopathogen causing the fire blight disease. The pathogen has a broad host-range affecting various *Rosaceae* (primarily Spiraoideae), including ecologically and economically important species (e.g.,apple and pear). The pathogenicity of *E. amylovora* is strictly dependent on a functional type III secretion system (T3SS) and the production of the exopolysaccharide amylovoran (Oh and Beer, 2005). We recently identified three T6SSs (T6SS-C1-T6SS-C3) in *E. amylovora* CFBP 1430 that differ in core and accessory gene content as well as gene organization (Smits et al., 2010b). T6SS-C2 (EAMY_1620- 1623) is constituted of four genes and hence not a complete T6SS gene cluster. Therefore we focused on T6SS-C1 and T6SS-C3 (EAMY _3003-3028 and EAMY_3201- 3228) (Fig. 1). Both T6SS gene clusters possess one *hcp* and two *vgrG* genes, with no evolved effector domains. Genes coding for potential signal transducers (serine/threonine phosphatase and serine/threonine kinase) are present in T6SS-C1, but absent in T6SS-C3. T6SS-C1 and T6SS-C2 were identified in other *Erwinia* species, whereas the third cluster is not present in all of the astrains (De Maayer et al., 2011). In this study, the aim was to analyze a potential contribution of the T6SSs of *E. amylovora* in virulence and to use RNA-seq to analyze transcriptomic changes. The performed plant assays indicated a minor contribution of T6SSs to the virulence of *E. amylovora*. Differential expression of motility and chemotaxis genes were observed, and further experiments showed that the T6SSs have an effect on the motility of *E. amylovora* CFBP 1430.

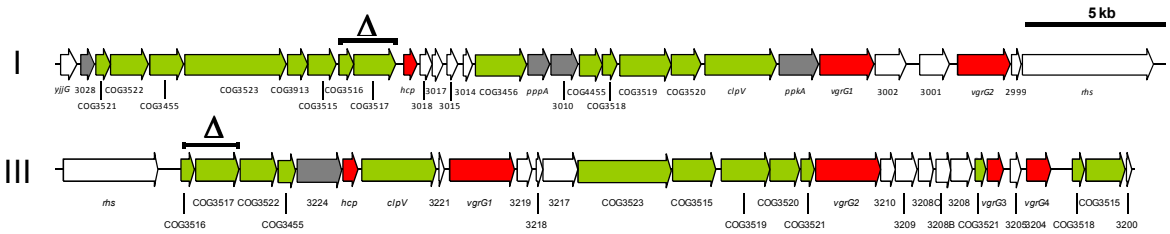

Figure 1 Type VI secretion systems gene clusters of *E. amylovora* CFBP 1430. Core genes are depicted in green, putative effectors in red, conserved genes found in homologous clusters in grey. Deleted genes used in this study are marked with a bar and a Δ.

Material and Methods

Bacterial strains, media and growth conditions

E. amylovora strain CFBP 1430 was used for this study (Table 1). The strain was routinely grown on KB or LB plates with the addition, where necessary, of chloramphenicol (20 µg/ml) and ampicillin (200 µg/ml). For flower population studies, NSA plates containing actidione (50 mg l^{-1}) were used. Liquid cultures were grown to the mid-log phase at 28 °C with continuous shaking. Cells for RNA extraction were either grown in M9 (sucrose added as carbohydrate source), LB, KB, M63 (glucose added as carbohydrate source) or HrpMM (either sorbitol or glucose was added as carbohydrate source). All carbohydrate sources had a final concentration of 2%.

Construction of T6SS mutants

The lambda red recombination system (Datsenko and Wanner, 2000) was used to generate Δ*duf*770, *duf*877 mutants of T6SS cluster 1 and 3 (EAMY_3020-3021, EAMY_3227-3228). Plasmids utilized are listed in Table 1. Plasmid pKD3 was used as template to amplify the chloramphenicol resistance cassette with the primer pairs listed in Table 2. PCR products were introduced by electroporation into competent *E. amylovora* CFBP 1430 cells carrying plasmid pKD46. The single mutants were constructed by deletion of the complete reading frames of *duf*770/*duf*877 in each cluster. To create the double mutant the plasmid pKD46 was removed from the cluster 1 mutant by incubation on LB plates at 37 °C overnight and colonies were screened for loss of antibiotic resistance. Plasmid pCP20 was introduced to eliminate the chloramphenicol resistance cassette. Plasmid pCP20 was removed by incubation on LB plates at 37 °C overnight and colonies were screened for loss of antibiotic resistance.

Plasmid pKD46 was transformed into the recovered colonies and mutation of *duf*770/*duf*877 in cluster 3 was performed as described above.

Table 1 *E. amylovora* strain and plasmids used in this study.

Strain or plasmids		Description	Reference
CFBP 1430		Wild type strain	(Smits et al., 2010b)
ΔT6SS-C1		Δ*duf770*, *duf877* (EAMY_3020-3021) in T6SS cluster 1	This study
ΔT6SS-C3		Δ*duf770*, *duf877* (EAMY_3227-3228) in T6SS cluster 1	This study
ΔT6SS-C1C3		Δ*duf770*, *duf877* (EAMY_3020-3021 and ΔEAMY_3227-3228) in T6SS cluster 1 and cluster 3	This study
pKD46	ap^R	Red recombinase expressing plasmid	(Datsenko and Wanner, 2000)
pKD3	ap^R, cm^R	Antibiotic resistance cassette template	(Datsenko and Wanner, 2000)
pCP20	ap^R, cm^R	FLP encoding recombinase plasmid	(Datsenko and Wanner, 2000)

ap^R : ampicillin resistance

cm^R: chloramphenicol resistance

RNA isolation and reverse transcription RT-PCR

RNA was extracted from bacteria grown to the mid-log phase in liquid media. The NucleoSpin RNA II kit (Machery Nagel) was used for RNA isolation, following the manufacturer's instructions. Flowers were inoculated with a pipette applying 5 µl of bacterial suspension containing 10^7 cfu ml^{-1} to the hypanthium. The flowers were collected 2 DPI, petals were removed and washed in water. The floral parts were removed from the solution and centrifuged. The supernatant was discarded, the pellet flash-frozen in liquid nitrogen and stored at -86 °C until RNA-extraction. Total RNA was isolated using the innuPREP Plant RNA Kit (Analytikjena, Germany) according to the manufacturer's instructions. All total RNA samples were treated with DNase I (Thermo Scientific, Wohlen, Switzerland) and control PCRs were performed to check for DNA contamination. For RT-PCR samples the RevertAid H Minus First Strand cDNA Synthesis Kit (Fermentas) was used to create cDNA templates. Qualitative PCR with specific primer pairs (Table 2) was performed. Quality and concentration of the RNA samples were determined using the Bioanalyzer 2100 (Agilent Technologies, Stuttgart, Germany). Samples were pooled to the required amount for further processing.

RNA-seq data analysis

RNA-seq reads were mapped to the *E. amylovora* CFBP 1430 genome sequence (Smits et al., 2010b) with bowtie version 0.12.7 (Langmead et al., 2009). Analysis of differential expression levels was performed using Cufflinks version 1.3.0 (Trapnell et al., 2010). Gene expression levels were normalized using fragments per kilobase of exon per million mapped reads (FPKM) report values. Genes were considered as up- or down-regulated, when their fold change was ≥ 1.5 or ≤ -1.5, respectively, and their P value < 0.001.

Immature pears assay

E. amylovora WT and mutants were grown over-night, collected by centrifugation and adjusted to cell-densities of approximately 10^3, 10^5 and 10^7 cfu ml^{-1}. The pears were surface sterilized using 10% bleach, pierced with a needle and subsequently inoculated with 5µl bacterial suspension. The fruits were incubated in a humidity chamber at 28 °C for 8 days. Fruits were assayed in triplicates for each treatment and the experiment was repeated twice.

Shoot inoculation assay

One year old grafted apple shoots (*Malus x domestica*, 'Golden Delicious') and pear shoots (*Pyrus communis*, 'Conference') were used for inoculation experiments. Shoots were inoculated with a syringe with a bacterial suspension containing approximately 10^8 cfu ml^{-1}. The plants were assayed in pentaplicates with five repetitions. Symptoms were recorded over a period of four weeks and the lesion length percentage was calculated. The data was log transformed before the two way Anova and Fisher's least significant difference test, at a significance level of 5% was performed using the Sigmaplot software 10 (Systat Software).

Flower assay

Three two year old grafted apple (*Malus x domestica***,** 'Golden Delicious') flowering trees were spray-inoculated using an atomizer. The bacterial suspensions contained approximately 10^7 cfu ml^{-1}. To determine bacterial population sizes the petals were removed and the remaining flower parts were washed in water. Bacteria were plated immediately after inoculation and at 24, 48 hours post inoculation. Three flowers per tree were assessed to determine the population sizes. Flower necrosis were rated 10, 12 days post inoculation. The experiment was repeated twice. A total of 529 (WT), 629 (ΔT6SS-C1), 543 (T6SS-C3) and

580 (ΔT6SS-C1C3) flowers were rated. A *t*-test ($p < 0.05$) was applied to identify statistical significant differences between the treatments using the Sigmaplot software.

Table 2 Primers used in this study

Mutations of *duf770/duf877*		
	Forward	**Reverse**
ΔT6SS-C1	ATGGAGAACACCATGGCAGTCAGTAAA TCCAGTGGGCAGAAATTCATTGCgtgtaggc tggagctgcttc*	TCACGCGTCGTTCGATTTCAGCGACGGC AGTTTAGAAACCAGACGCAGTGcatatgaat atcctcctta*
ΔT6SS-C3	ATGTCTAACTCCTGGCAGTCCGAGATCC CCAAGGCTCGCGTTAACATTCA gtgtaggctggagctgcttc*	TTATGCCTTGGCTTTTGGCATCTGCGAC ACCAGCGACAGATTGACGTCCA catatgaatatcctcctta*
Reverse-transcription PCR		
	Forward	**Reverse**
hcp1	ACACCGGTTGGATCGACGTGTCT	CGGAGGTGCTCTGCTCCCAGTAC
hcp2	TCTCTCGCAGGATCATAGCCTGT	GATTCTGTACCACTTGAACTCGG
recA	CCATCATGCGCCTGGGTGAAGAC	CGGCATCGATAAACGCACAGGTC
dspA/E	GGGCATGGTGTTGCCTTACAGC	GCGCCAGCAGATCGCGCAATGTT
duf879-1	GAGATGATTGCGCCGAACTACCT	GTACCGGTTGCAGCATCACATCG
vgrG4	AGCTGACCAGTCGCACTACACAA	TTCCGCACCGTCGAACAACCCAG
duf879-2	GACCCGTACGTCGAACGCCTGTT	CTCCGACAGACACTCAGACTGGC
ffh	CGATAGACTATCGCAAACCCTG	TTCACTTCCTGACCAACGGC
foxR	TGACTCGTCAGCAGATGGAAGAT	TTGAAGCTACCCGGATCGCTCAT
hrpL	GAAGGCATATTCCGTGAGCAT	TGAGTCAGGATGATATCGTCTTC

* Lower case letters indicate sequences for amplification the chloramphenicol resistance cassette of pKD3

Motility assay

Twenty microliters of a 10^8 cfu ml^{-1} containing suspension in 0.8% NaCl solution was placed on soft agar plates (3 g L^{-1} agar, 10 g L^{-1} plant tryptone, 5 g L^{-1} NaCl). Bacterial strain were freshly plated form glycerol stocks kept at -86° C and grown overnight on KB plates. The motility agar plates were assessed after two days of incubation at 28 °C.

Results

Characterization of T6SS mutants

In order to assess whether the T6SS-C1 and T6SS-C3 contribute to the virulence of *E. amylovora* CFBP 1430, deletion mutants were constructed applying the lambda red recombination system (Datsenko and Wanner, 2000). The consecutive core genes *duf770* and *duf877* were replaced by an antibiotic resistance cassette in either (resulting single mutants named ΔT6SS-C1 and ΔT6SS-C3) or in both T6SS clusters (resulting double mutant named ΔT6SS-C1C3). To exclude differences in growth rates, growth curves were determined in different media (KB, M9, HrpMM, synthetic nectar). No obvious differences were detected. In order to analyze the expression of a set of selected T6SS genes (T6SS-C1 (*hcp1*, *duf879*), T6SS-C3 (*hcp2*, *vgrG4*, *duf879*)), RNA was isolated from *E. amylovora* CFBP 1430 grown in the same media to the mid-log phase, and subsequent qualitative assessment showed no difference in expression.

In vitro transcriptome WT versus ΔT6SS-C1C3

RNA was isolated from WT and ΔT6SS-C1C3 mutant strains of *E. amylovora* CFBP 1430, grown in minimal sucrose M9 medium. The cDNA libraries (ribosomal RNA depleted) were constructed and Illumina sequenced leading to 18,598,523 (WT) and 18,275,977 (ΔT6SS-C1C3) reads and filtered for adapter sequences resulting in 17,321,715 (WT) and 17,310,909 (ΔT6SS-C1C3) reads. Alignment of these reads to the *E. amylovora* CFBP 1430 genome sequence had an overall alignment rate of 91.43% (WT) and 91.04% (ΔT6SS-C1C3). The resulting data set consists of 3,705 expressed genes; five genes that code for hypothetical proteins were not expressed in the WT nor ΔT6SS-C1C3. Analysis of the mapped reads showed that the mutations led to significant differential expression of 508 genes in comparison to the WT. (suppl. Table 1, see appendix), of these genes 391 have an annotation and 117 are predicted to encode for hypothetical proteins. The differential expressed genes were classified into groups according to their gene ontology terms (Fig. 2). Processes affected include the categories cellular process, metabolic process, pigmentation, response to stimulus, biological regulation, localization and locomotion.

Genes of the hypersensitive response and pathogenicity (Hrp) cluster (*hrpK*, *hsvA*, *hrpA1*, *hrcJ*, *hrpD*, *hrpE*, *hrcC*, *hrpF*, *hrpG*), the putative effector *hopPtoC*, and genes of the two Inv/Spa-type III secretion systems (PAI-2, PAI-3) (*prgH1*, *sipB1*, *spaI1*, *spaK*, *spaM1*, *spaN1*, *spaO1*, *spaP1*, *spaQ1*, *spaT1* and *prgJ3*, *prgK3*, *invA3*, *invB*, *spaS3*) are differentially

expressed. The transcripts of the Hrp gene cluster had a lower transcript abundance in the ΔT6SS-C1C3 mutant than transcripts of the WT, with the exception of *hrpK* which showed higher abundance. The genes of the PAI-2 Inv/Spa cluster had a higher transcript abundance, and the PAI-3 Inv/Spa lower, except for *spaK* which was higher.

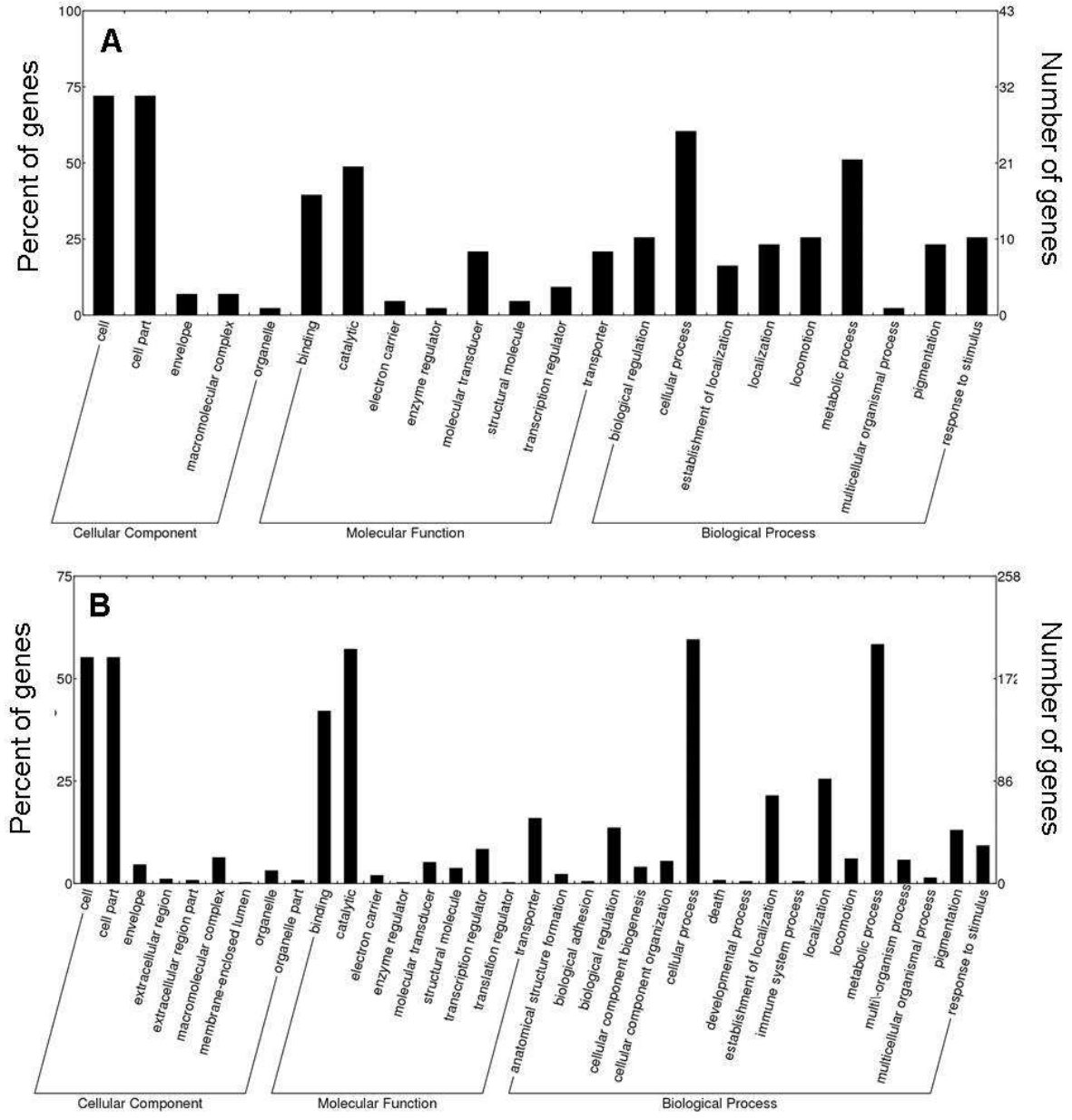

Figure 2 Significantly differentially expressed genes categorized according to their GO annotation. Only genes with GO annotation are represented. The *in planta* transcriptomic data are depicted in the graph on top **(A)** and the *in vitro* data in the bottom graph (**B**).

Pathogenicity associated genes like amylovoran biosynthesis (*amsK*, *amsL*, *amsJ*) and fitness factors like desferrioxamine siderophore (Fe^{3+} uptake) biosynthesis (*dfoJ*) are also influenced by the mutations. The transcripts levels of *amsK* and *amsL* were lower and *amsJ* was higher in the ΔT6SS-C1C3 mutant compared to the WT. Transcripts of the two sets of flagellar genes

were differentially expressed, most biosynthetic and associated chemotaxis and motility (*fli*, *flh* and *flg* and all *mot* and *che*) genes had a higher transcript abundance in the ΔT6SS-C1C3 mutant than in the WT, except the biosynthesis genes *fliQ3*, *fliR3* and transcriptional regulators *flhD3* and *flgM* which were lower.

Immature pear assay

To get a first indication if T6SS is involved in pathogenicity of *E. amylovora* CFBP 1430 an immature pear assay was performed. WT, ΔT6SS-C1, ΔT6SS-C3, and ΔT6SS-C1C3 were assessed for altered virulence on immature pear fruits (cv. 'Conference'). The WT and the mutants were applied at different concentrations and were assessed 8 days post inoculation (DPI). The application of 10^7 and 10^5 cfu ml^{-1} led to similar tissue maceration and ooze production of all the mutants compared to WT. No symptoms for neither of the strains could be observed when 10^3 cfu ml^{-1} was applied.

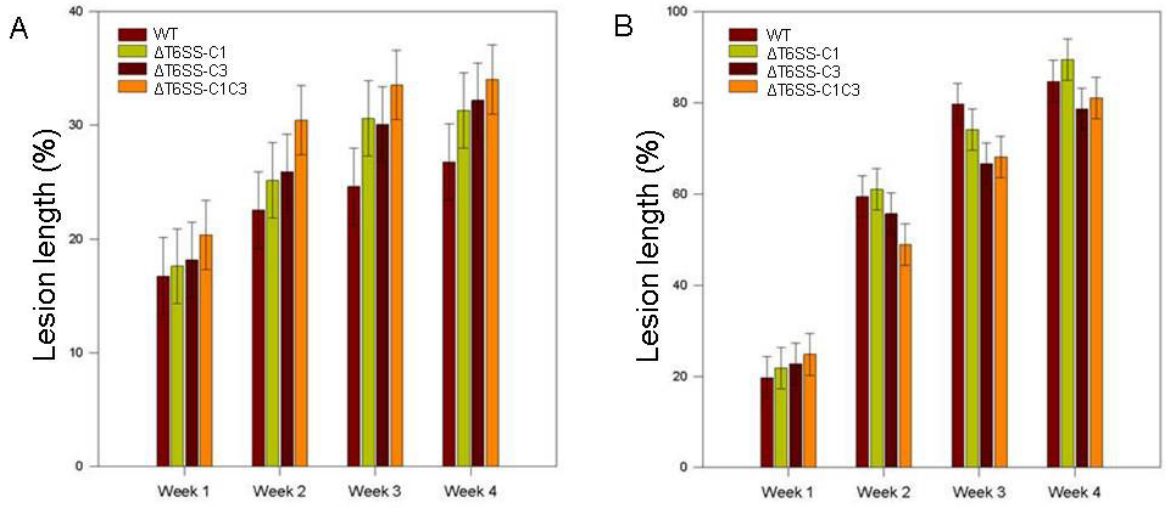

Figure 3 Role of T6SS in virulence on apple (**A**) and pear (**B**) plants. Shoots were inoculated with a bacterial suspensions containing approximately 10^8 cfu ml^{-1} of a single strain derivative. Disease progression was measured once a week for four weeks. Values of percent lesion length represent the means of 25 replicate plants with standard deviation.

Shoot inoculation

To further characterize the mutants, shoots of apple (cv. 'Golden Delicious') and pear (cv. 'Conference') shoots were inoculated either with the WT or one of the three T6SS mutants. The necrotic lesions were recorded weekly during 4 weeks. The percent lesion length was calculated by dividing the lesion length by the shoot length. Disease development as well as disease progression in pear shoots showed no significant difference between WT and the

T6SS mutants. In apple shoots, the ΔT6SS-C3 and the ΔT6SS-C1C3 mutant exhibit a significant increase in necrotic lesion length compared to the WT and ΔT6SS-C1 mutant (Fig. 3). Percentage lesion length caused by the ΔT6SS-C1C3 mutant was highest throughout the experiment.

Flower assay

Flowers are the primary infection court of *E. amylovora* in the naturally occurring situation. The pathogen is able to invade host planthost plants through the nectaries, thus no wounding of plant tissue as with artificial inoculation occurs. Freshly opened apple flowers ('Golden Delicious') of flowering trees were inoculated with bacterial suspensions (WT and T6SS mutants) containing 10^7 cfu ml^{-1}. Population sizes for all strains were determined 1 DPI and 2 DPI to check altered growth patterns. No significant differences could be detected. The flowers, scored after 10 DPI (12 DPI), showed a significant reduction of ~20% necrotic lesion for the ΔT6SS-C1C3 compared to the WT (Fig. 4). The ΔT6SS-C1 and ΔT6SS-C3 single mutants showed a slight, but insignificant reduction of necrosis.

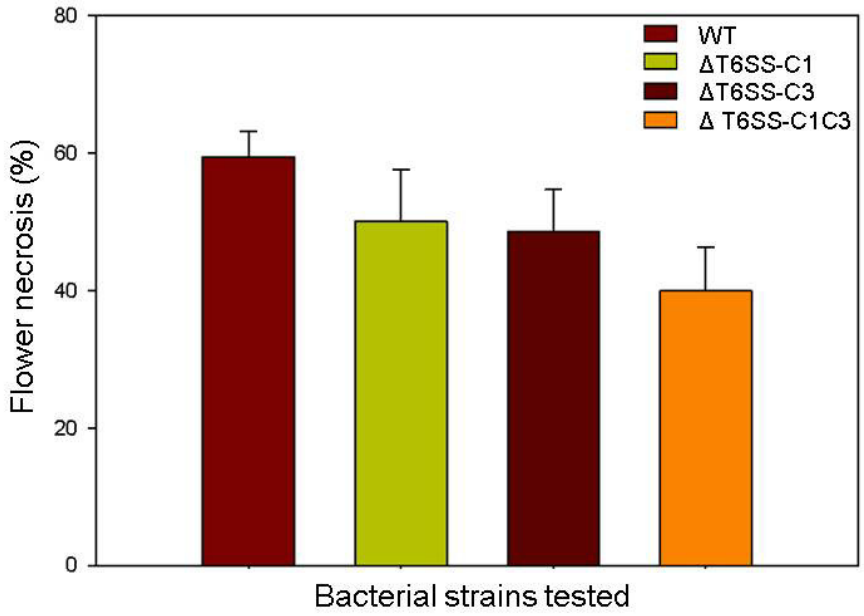

Figure 4 Role of T6SS in disease development on apple flowers. Flowers were inoculated with a bacterial suspensions containing approximately 10^7 cfu ml^{-1} of a single strain derivative. Disease symptoms were rated 10, 12 days post inoculation. Bars with standard deviation represent the means of two independent experiments.

In planta transcriptome WT versus T6SS double mutant

Flowers of the susceptible cultivar 'Golden Delicious' were inoculated with either the WT or ΔT6SS-C1C3 variant of *E. amylovora* CFBP 1430. Bacterial cells were recovered 2 DPI for RNA extraction, cDNA library preparation and subsequent Illumina sequencing. A total of 44,296,072 (WT inoculated sample) and 45,470,859 (ΔT6SS-C1C3 inoculated sample) reads were mapped to the *E. amylovora* CFBP 1430 genome sequence with an overall alignment rate of 10.65% and 20.77%. The low alignment rate was due to cDNA derived from apple. Mapping of the reads to the apple genome sequence revealed that approximately 86.92% (WT inoculated sample) and 77.28% (ΔT6SS-C1C3 inoculated sample) aligned to it.

The bacterial transcriptome includes 3,563 expressed genes, transcripts of 141 genes are found in none of the conditions. Most of the 141 genes encode hypothetical proteins, five have an annotation (*flgB3*, *glcG*, *intS1*, *spaR3*, *yeeV*). Among the non-expressed genes a flagellar (*flgB3*), a fimbrial (EAMY_0247) and a type III secretion system (*spaR3*) gene were identified. These genes were found to be expressed *in vitro* (only *intS1* differentially). The differential expressed genes were grouped according to their GO annotations (Fig. 2). The biological processes include the categories cellular process, metabolic process, pigmentation, response to stimulus, biological regulation, and localization and locomotion.

Analysis of the reads that mapped onto the *E. amylovora* CFBP 1430 genome sequence showed that the mutations led to significant differential expression of 56 genes in comparison to the WT. Of these56 genes, 49 are annotated and seven encode hypothetical gene products (suppl. Table 2, see appendix). The mutations influence the processes phosphate transport (*pstA3*, *pstC3*, *pstS3*), sulfur metabolism (*cysC*, *cysI3*, *cysJ*, *cysN*, *tauA*, *tauB*, *tauC*, *tauD3*), chemotaxis (*cheA1*, *cheB1*, *cheR1*, *cheY1*, *cheZ1*) and cell motility (*motA1*, *motB1*) and were identified to be differentially expressed. All chemotaxis, cell motility as well as the transport and sulfur metabolic genes had a lower transcript abundance in ΔT6SS-C1C3 compared to the WT. Some of these genes were identified to be differentially expressed in the *in vitro* transcriptome as well (*cheB1*, *cheR1*, *cheY1* and *motA1*, *motB1*).

Motility assay

The *in vitro* and *in planta* transcriptome data implied that chemotaxis and motility might be altered in the ΔT6SS-C1C3 mutant. To test for a phenotypic effect, a motility assay was performed including the single mutants ΔT6SS-C1 and ΔT6SS-C3. The ΔT6SS-C1 mutant showed an asymmetric, the ΔT6SS-C3 and ΔT6SS-C1C3 no motility 2 DPI compared to the

WT (Fig. 5). The differences in motility did not arise from differential growth rates in the media used, as WT and all T6SS mutants grew at similar rates and to similar densities (data not shown).

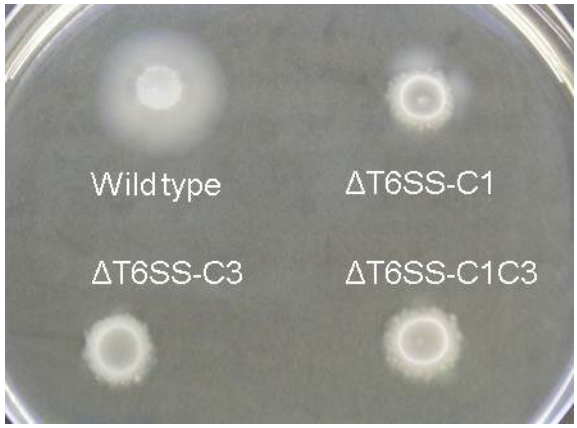

Figure 5 Comparison of motility of wild type and T6SS mutants. Stains were inoculated onto semi-solid agar and motility diameters were assessed 2 days post inoculation

Discussion

Type III secretion system related proteins and the exopolysaccharide amylovoran are known to be important virulence factors of *E. amylovora*. The recent publication of *E. amylovora* genome sequences allows the assessment of the complete arsenal of factors required for full virulence and ecological competitiveness of the pathogen. We recently identified three T6SSs (T6SS-C1-T6SS-C3) in *E. amylovora* CFBP 1430 (Smits et al., 2010b; De Maayer et al., 2011). T6SS gene clusters have been identified in many Gram-negative bacteria, but although an evolutionary genetic conservation of T6SS genes deletion mutants led to varying phenotypes dependent on the bacterial species. Evidence suggests that in some bacteria, e.g., *Burkholderia mallei* ATCC 23344, *Vibrio cholerae* V52 and *Edwardsiella tarda* EIB202, the T6SS is a virulence factor (Pukatzki et al., 2007; Schell et al., 2007; Wang et al., 2009b). However, T6SS have been identified in non-pathogenic bacteria as well, suggesting that these systems have additional functions. This is supported by the fact that T6SS in the endosymbiont *Rhizobium leguminosarum* RBL5523 is involved in host specificity; deletion of a T6SS gene allowed the formation of nitrogen fixation–competent nodules on non-host plants (Bladergroen et al., 2003). The T6SS in *Pseudomonas aeruginosa* PAO1 mediate inter-bacterial interactions by targeting toxic compounds to other bacterial cells by a toxin-immunity system (Hood et al., 2010).

For only a few plant pathogenic bacteria, including *Pectobacterium atrosepticum*, *Agrobacterium tumefaciens*, and *Pseudomonas syringae,* functionality of T6SS was demonstrated. Transcriptome and secretome analyses of *P. atrosepticum* SCRI1043 and *A. tumefaciens* C58 identified T6SS genes and proteins to be induced and secreted under plant mimicking conditions (Mattinen et al., 2007; Mattinen et al., 2008; Wu et al., 2008; Yuan et al., 2008). The deletion of *hcp* in *A. tumefaciens* led to a reduced tumorgenesis in plant assays, whereas in *P. atrosepticum* SCRI1043, deletion mutants showed increased or slightly reduced virulence dependent on the deleted gene (Liu et al., 2008; Mattinen et al., 2008). Given the diversity of functions in other bacterial species, we tested the contribution of T6SS in *E. amylovora* CFBP 1430 to virulence and potential influence on the transcriptome by plant assays and RNA-seq.

The comparison of the transcriptomic data obtained from the *in vitro* cultured wild type and ΔT6SS-C1C3 showed that virulence associated genes, e.g., Hrp T3SS associated, amylovoran biosynthesis, as well as a set of flagellar genes are differentially expressed. This indicated that the mutation of T6SS genes influenced the expression of the afore mentioned genes under the conditions tested. To assess if the transcriptional changes *in vitro* might influence virulence in host plant, we performed three plant assays (immature pear, shoot and apple flower inoculation) to cover different plant organs that might be affected by the T6SS of *E. amylovora* CFBP 1430. Shoot assays were additionally performed in pear and apple plants to assess a potential effect on host-specificity. The inoculation with wild type and T6SS mutant derivatives of pear shoots and immature pear assays showed no difference in disease and symptom development. Similar results were obtained for T6SS mutants of *P. syringae* pv. *Syringae*, where infiltration of the mutant derivative into bean plants did not alter virulence of the pathogen (Records and Gross, 2010). The apple shoots and flower inoculation experiment showed opposing results. The ΔT6SS-C1 and ΔT6SS-C1C3 showed increased symptom development in apple shoots compared to the WT. On flowers, the symptoms caused of ΔT6SS-C1C3 were reduced compared to the *E. amylovora* CFBP 1430 wild type strain. In other bacteria like *Legionella pneumophila* ATCC33152, *Salmonella typhimurium* ATCC 14028, and *P. atrosepticum* SCRI1043 mutations in T6SS genes affected intracellular growth and led to altered replication rates (Zusman et al., 2004; Parsons and Heffron, 2005; Mattinen et al., 2008). We excluded that the effects on virulence were cause by differential replication rates, since all the T6SS mutants had similar growth rates and grew to same cell densities *in vitro* and *in planta*. The influence on virulence was moderate compared to main factors like the Hrp-type III secretion system and the exopolysaccharide amylovoran (Bellemann and

Geider, 1992; Kim and Beer, 1998). The results suggested that the differences in virulence (increase, decrease respectively) in apple shoots and on flowers were dependent on the ΔT6SS-C3 and that T6SSs influence the onset and disease progression in apple shoots. In apple flowers, the ΔT6SS-C1C3 mutant showed a significant reduction in flower necrosis. The transcriptome data generated from RNA-sequencing indicated that chemotaxis and motility genes had a lower transcript abundances *in planta* and the motility plate assay confirmed that the T6SS mutants are impaired in motility. Motility of *E. amylovora* CFBP 1430 was demonstrated to be an important trait to invade non-injured apple leaves, whereas no significant effect could be detected on injured plants (Cesbron et al., 2006). Thus, the impaired motility of the T6SS mutants *in vitro* might also influence the invasion process on flowers leading to less necrosis compared to the WT. Alternatively the T6SS might delay or promote disease development dependent on the plant organ affected.

The trancriptomic data obtained from flower inoculation experiments additionally showed that metabolic processes were affected, namely phosphate transport and sulfur metabolism. Under the tested conditions, the genes of these pathways had a lower transcript abundance in the ΔT6SS-C1C3 mutant than in the WT indicating an influence on metabolic functions on apple flowers. Sulfur and phosphate are two essential nutrients for growth and cell functions, but the lower expression of these genes did not significantly influence flower colonization.

The deletion of structural T6SS genes of *E. amylovora* CFBP 1430 led to multiple effects. It promoted virulence in apple shoots and reduced flower necrosis. Additionally, the T6SSs mutants were impaired *in vitro* in their motility which might be the case in the floral court as well hindering the invasion process. The comparison of the transcriptomic data (*in vitro* versus *in planta*) revealed a small overlap of differentially expressed genes. The differing transcriptional changes included virulence associated genes *in vitro* (e.g., amylovoran biosynthesis, T3SS) indicating an influence of T6SS on different processes dependent on the environmental and growth conditions.

Chapter 4

Characterization of the antibacterial peptide herbicolin I biosynthetic operon in *Pantoea vagans* biocontrol strain C9-1 and incidence in *Pantoea* species

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Characterization of the antibacterial peptide herbicolin I biosynthetic operon in *Pantoea vagans* biocontrol strain C9-1 and incidence in *Pantoea* species

Abstract

Pantoea vagans C9-1 is a biocontrol strain that produces at least the two antibiotics inhibiting the growth of *Erwinia amylovora*, the causal agent of fire blight disease of pear and apple. One antibiotic, herbicolin I, was purified from culture filtrates of *P. vagans* C9-1 and determined to be 2-amino-3-(oxirane-2,3-dicarboxamido)-propanoyl-valine also known as Nß-epoxysuccinamoyl-DAP-valine. A plasposon library was screened for mutants that lost the ability to produce herbicolin I. It was shown that mutants had reduced biocontrol efficacy in immature pear assays. The biosynthetic gene cluster in *P. vagans* C9-1 was identified by sequencing the flanking regions of the plasposon insertion sites. The herbicolin I biosynthetic gene cluster consists of 10 CDS and is located on the 166-kb plasmid pPag2. Sequence comparisons identified orthologous gene clusters in *P. agglomerans* CU0119 and *Serratia proteamaculans* 568. A low incidence of detection of the biosynthetic cluster in a collection of 45 *Pantoea* spp. from biocontrol, environmental, and clinical origin showed that this is a rare trait among the tested strains.

Introduction

Erwinia amylovora, the causal agent of the fire blight disease, is a major threat to pome fruit production. The pathogen colonizes flowers and, under favorable weather conditions, enters through the nectarthodes, kills tissues, and spreads throughout the (Rosen, 1935; Thomson, 1986). Until now, no cure for infected plants is known and diseased tissues have to be removed by pruning. Measures to reduce disease incidence include antibiotic and biocontrol agent application during bloom. The emerging resistance of *E. amylovora* to the most effective antibiotic streptomycin (Loper et al., 1991; Chiou and Jones, 1995) raises the need for further management measures. Application of biocontrol agents of the related enterobacterial genus *Pantoea* can remarkably reduce epiphytic growth of the pathogen (Stockwell et al., 2002; Anderson et al., 2004; Francés et al., 2006; Pusey et al., 2008; Stockwell et al., 2010). Site exclusion, nutrient competition, and antibiotic production contribute to the effectiveness of biocontrol agents (Vanneste et al., 1992; Kearns and Mahanty, 1998; Vanneste et al., 2008; Pusey et al., 2011).

Pantoea vagans C9-1, recently reassigned from the closely-related *Pantoea agglomerans* (Rezzonico et al., 2009), is an effective biocontrol agent inhibiting the growth of *E. amylovora in vitro* (Ishimaru et al., 1988) and in orchard trials (Stockwell et al., 2010, 2011). The biosynthesis of at least two antibiotics contributes to the suppression of *E. amylovora* in immature pear assays (Ishimaru et al., 1988). The effectiveness of *P. vagans* C9-1 was evaluated in field trials resulting in a significant reduction of fire blight incidence (Stockwell et al., 2010, 2011). *P. vagans* C9-1 has been commercialized as BlightBan^{TM} C9-1 (NuFarm Americas, Burr Ridge, IL) for biocontrol of fire blight of pear and apple.

Many *Pantoea* species produce one or multiple antibiotics that are effective against fire blight, including a phenazine antibiotic produced by *P. agglomerans* Eh1087 (Giddens et al., 2002), pantocin A produced by *P. agglomerans* strains P10c and Eh318 and *Pantoea* sp. Eh252 (Stockwell et al., 2002; Jin et al., 2003; Vanneste et al., 2008; Rezzonico et al., 2009), and pantocin B produced by *P. agglomerans* Eh318 (Wright et al., 2001). Although the production of antibiotics is observed for many *Pantoea* species, the biosynthesis genes of only few have been identified (Giddens et al., 2002; Jin et al., 2003; Jin et al., 2006; Hollenhorst et al., 2010). The identification of antibiotic biosynthetic gene clusters allows the screen for potential antibiotic producing strains and to assess novel biocontrol agents.

The main objective of this study was to genetically and chemically characterize the antibiotic produced by *P. vagans* C9-1 given the common name herbicolin I. A recent study indicated that herbicolin I could be identical to 2-amino-3-(oxirane-2,3-dicarboxamido)-propanoyl-valine produced by *Pantoea agglomerans* 48b/90 (Sammer et al., 2009), of which the biosynthetic genes were to date unknown. This study confirms the chemical structure of herbicolin I, while the gene cluster was identified using plasposon mutants. The analysis of the biosynthetic genes revealed a similar gene cluster in *P. agglomerans* CU0119, which produces a family of dapdiamide antibiotics (dapdiamide A-E) (Hollenhorst et al., 2009; Dawlaty et al., 2010). Additionally, we evaluated the incidence of homologous biosynthetic genes across a wide-range of *Pantoea* spp. including plant, environmental, and clinical isolates.

Materials and Methods

Bacterial strains and plasmids

P. vagans C9-1, originally isolated from apple (*Malus* x *domestica* 'Jonathan', MI, USA) (Ishimaru et al., 1988), was used throughout. Additional bacterial strains used are listed in Table 1. *Escherichia coli* S17-1 λ*pir* was used for transformation of rescued pTn*Mod*-RKm' plasposons (R6K *ori*, Tn*Mod*, Km^r, RP4, *oriT*, Tn5*tnp*). All strains were stored at -80°C and routinely cultured in Luria-Bertani (LB) medium. *E. coli* was cultured at 37°C and all other strains were cultured at 26°C. Kanamycin (Km) was used at a concentration of 50 μg ml^{-1} as appropriate.

Antimicrobial production and activity assays

Antibiotic production was examined in a double diffusion assay on MGA medium [MOPS (morpholino-propane sulfonic acid), gluconate, asparagine medium)] at 26°C (Ishimaru et al., 1988). Bacteria were grown 18 to 24 h in LB or LB-Km medium for mutants. A 10 μl cell suspension (0.1 OD_{600nm}) was spotted onto the basal MGA layer. The colonies were grown for 48 h, exposed to chloroform and subsequently overlaid with molten MGA agar seeded with wild type *E. amylovora* Ea110, pantocin A (CIR555) and herbicolin I (CIR550) resistant mutants (Ishimaru et al., 1988). The overlays were incubated for 48 h and visually inspected for zones of inhibition. Antimicrobial activity of purified antibiotics was assayed similarly except test samples were spotted on MGA agar and dried before being overlaid with an indicator strain.

Mutational analysis

Plasposon mutants of *P. vagans* C9-1 were generated according to the method of Dennis et al. (8). Briefly, pTn*Mod*-RKm' was introduced into *P. vagans* C9-1 cells by electroporation. Mutants containing the pTn*Mod*-RKm' were selected on LB agar containing Km. Antibiotic deficient mutants were identified by their inability to form a zone of inhibition against the pantocin A-resistant *E. amylovora* CIR555. Genomic DNA of the herbicolin I mutants containing pTn*Mod*-RKm' was isolated using the method of Desomer et al. (Desomer et al., 1991). The genomic DNA was digested with the restriction enzyme *Pst*I, self-ligated overnight and transformed into *E. coli* S17-1 λ*pir*. Replicating plasmids were recovered and the flanking regions were sequenced using the primers TnMod_FP-1 and TnMod_RP-1

(Table 2). Sequences were identified in the published genome sequence of *P. vagans* C9-1 plasmid pPag2 (GenBank Acc. No. CP001894) (Smits et al., 2011).

Immature pear fruit assay

Inhibition of *E. amylovora* by *P. vagans* C9-1 and its antibiotic-deficient derivatives was tested in immature pear fruit (Rezzonico et al., 2007). Fruit surfaces were disinfected with 70% ethanol, bisected longitudinally, and placed on sterile, moistened Whatman filters in Petri dishes. A 50 µl suspension of *P. vagans* in 5 mM phosphate buffer (pH 6.5) at 5 X 10^5 cfu ml^{-1} or 5 X 10^6 cfu ml^{-1} or buffer alone was introduced into a 5-mm-deep-well in each pear half with a sterile pipette tip, and left to absorb for 2 h. A 50 µl suspension of *E. amylovora* (5 X 10^5 cfu ml^{-1}) in 5 mM phosphate buffer (pH 6.5) was introduced into the same well. Treatments consisted of six replicate pear fruit halves and each experiment was repeated three times.

Disease symptoms (necrosis and/or bacterial ooze) were first observed 2 days after inoculation and recorded daily over 5 days after inoculation. The incidence of disease was calculated for each treatment and day. Disease incidence was transformed into the arcsine square root for normalization prior to analysis with the analysis of variance (ANOVA) procedure of SAS (Statistical Analysis Systems, Cary, NC). Disease incidence data did not vary significantly among experiments and were pooled. Treatment means for each day were separated by Fisher's protected least significant difference test at $P = 0.05$.

Sequence analysis

The BlastN subroutine in GenDB (Meyer et al., 2003) was used to identify the insertion sites of the plasposons in the genome sequence of *P. vagans* C9-1 (Smits et al., 2011). Routine sequence manipulations were done using the subroutines of the Lasergene package version 8.1.5 (DNASTAR, Madison, WI, USA). Additional Blast searches (Altschul et al., 1990) were done at NCBI.

Antibiotic purification

Herbicolin I was purified from culture supernatants of *P. vagans* C9-1 by a combination of cation exchange chromatography, reverse phase HPLC, and instant thin layer chromatography (ITLC). Cells of C9-1 were grown until late log phase in 10 L MGA. Samples of concentrated supernatants were adjusted to pH 2.5 with 5 N H_2SO_4, and quickly added to a 5.5 cm x 10 cm

column of Dowex 50W x 4 (200-400 mesh) equilibrated in 2.5 mM ammonium acetate buffer (pH 5). After washing with 2.5 mM ammonium acetate buffer, antibiotics were eluted with 20 mM ammonium acetate buffer (pH 5), concentrated to dryness under reduced pressure at 40°C, and then resuspended in distilled water. Preparations were kept frozen at -20°C. Active fractions were applied to octydecyl (C_{18}) bonded phase sorbent packed in a 100 ml flash chromatography column and equilibrated in 0.1% (v/v) trifluoroacetic acid (TFA) in water. The column was eluted with 0, 5, 10, 20, and 50% methanol in 0.1% TFA and fractions immediately adjusted to a pH of 3.5-4.0 with 2% ammonium hydroxide. Fractions with antibiotic activity were pooled and concentrated under reduced pressure. Following flash chromatography, the active component was further purified by high pressure liquid chromatography (HPLC) on a C_8 semi-preparative column (25 cm x 9.4 mm) eluted with acetonitrile:water:TFA (5:94.9:0.1).

Peaks at absorbance 215 nm were collected and adjusted to pH 3.5-4.0. After concentration, antibacterial activity of each sample was assayed. Samples with antibacterial activity were repeatedly lyophilized to remove salts. The active compound was finally purified on instant thin layer chromatography (ITLC-SA) papers developed in acetonitrile:water (80:20).

To determine pH stability, aliquots of samples were pH adjusted with 0.5 NH_2SO_4 and 2% NH_4OH, and after 2 h, neutralized with 1 M potassium phosphate buffer (pH 7.0), and adjusted to constant volume. Heat stability was determined by examining residual antibiotic activity in preparations heated at 95°C for 2 h in sealed vials. Beta-lactamase assays were made with penicillinase 1 (Sigma Chemical Co., St. Louis, MO) and were incubated for 1 h at 26 °C.

The ^{1}H-NMR spectra in D_2O were obtained on a Bruker WM-250 instrument (Bruker BioSpin Corporation, Billerica, MA) with suppression of the solvent HDO resonance signal. Molecular weight and chemical formula were obtained by fast atom bombardment mass spectrometry (FAB-MS) of intact, underivatized herbicolins (0.01 mg in 0.01 ml glycerol matrix). Amino acid composition and sequence of herbicolin I was determined by Edman degradations liberated as phenylthiohydantoin-amino acids and analyzed by HPLC.

Sensitivity of orchard isolates of *E. amylovora* to antibiotics of *P. vagans* C9-1

Thirty four streptomycin-sensitive isolates and 25 streptomycin-resistant isolates of *E. amylovora* from commercial orchards in the Pacific Northwest of the USA (Loper et al., 1991) were evaluated for sensitivity to the antibiotics of *P. vagans* C9-1 with the double

diffusion assay on MGA medium described above. L-histidine (10 mM) was added to the overlay medium in replicate plates for each isolate to suppress antibiosis due to production of pantocin A. Additionally, isolates of Ea153 that were recovered from 20 diseased blossom clusters on pear trees treated twice with *P. vagans* C9-1 during bloom also were tested (Stockwell et al., 2011). Sensitivity assays were repeated twice.

Table 1 Primers used for sequencing the flanking regions of Tn*Mod* –RKm' and for prevalence screening

Primer Name	Sequence (5'-3')	Size (bp)	T_{anneal} (°C)
TnMod_FP-1	TCCCTCACTTTCTGGCTGGA	[a]	56
TnMod_RP-1	CCTCTCAAAGCAATTTTGAG		
ddaD_F	GGATCTTGCATCGTTCGCAC	807	58
ddaD _R	CGATCGCCTGTGCGGTAGTA		
ddaF_F	ATCCCTGCATTTCAGGCGCT	853	63
ddaF _R	ATGCCCCAGACACTCTTCGA		
paaA_fw	CTCTTGCCAAAATGGATGGT	2398	55
paaC_rev	TTGCAAATTCTGCACTCTCG		

[a] different amplicon sizes

Results

Chemical identification of antibiotic compound

The antibiotic referred to as herbicolin I was isolated from liquid cultures of *P. vagans* C9-1 and chemically characterized. The antibiotic was purified from culture supernatants of *P. vagans* C9-1 by a combination of cation exchange chromatography, reverse phase HPLC, and instant thin layer chromatography (ITLC). A different method than that of Sammer et al. (Sammer et al., 2009) was required to exclude the co-purification of pantocin A. The purified antibiotic was insensitive to beta-lactamase, base labile (pH>10), and heat and acid stable. The observed $[M+H]^+$ of the antibiotic was 317.14461 corresponding to a calculated $[M+H]^+$ of 317.14610 and a chemical formula of $C_{12}H_{21}N_4O_6$. The antibiotic contained the amino acid valine. The proton NMR spectrum of herbicolin I was identical to that of the dapdiamide produced by *P. agglomerans* 48b/90: 2-amino-3-(oxirane-2,3-dicarboxamido)-propanoyl-valine (Fig. 1) (Sammer et al., 2009).

Table 1*Pantoea* species collection used for prevalence screening of pantocin A and dapdiamide biosynthetic genes

Strain	Origin (reference)	Host	Properties	PCR data	
				paaABC[a]	***ddaD / ddaF***[b]
Pantoea vagans					
C9-1	USA (Ishimaru et al., 1988)	*Malus* x *domestica* (apple stem)	Biocontrol agent	+	+
C9-1W	Switzerland (Smits et al., 2010a)	N/A	Non-pigmented, pPag3 plasmid-cured variant of C9-1	+	+
LMG 24196	Argentina (Rezzonico et al., 2009)	*Eucalyptus* sp.	Phytopathogen	-	-
LMG 24199^T	Uganda (Rezzonico et al., 2009)	*Eucalyptus* sp.	Phytopathogen	-	-
Pantoea agglomerans					
CPA-2	Spain (Nunes et al., 2002)	*M. x domestica*(fruit surface)	Biocontrol agent	-	-
E325	USA (Pusey et al., 2008)	*M. x domestica*(flower)	Biocontrol agent	-	-
Eh1087	New Zealand (Kearns and Mahanty, 1998)	*M. x domestica*(flower)	Biocontrol agent	-	-
Eh239	USA (Braun-Kiewnick et al., 2000)	*Hordeum vulgare* (barley, kernel)	Biocontrol agent	-	-
Eh318	USA (Wright et al., 2001)	*M. x domestica*(stem)	Biocontrol agent	+	-
Eh454	USA (Braun-Kiewnick et al., 2000)	*H. vulgare* (kernel)	Biocontrol agent	-	-
Eh460	USA (Braun-Kiewnick et al.,	*H. vulgare* (kernel)	Biocontrol agent	-	-

	2000)				
P10c	New Zealand (Vanneste et al., 2002)	*M. x domestica*(flower)	Biocontrol agent	+	-
EPS125	Spain (Bonaterra et al., 2005)	*Pyrus communis* (pear, fruit surface)	Biocontrol agent	-	-
ATCC 27987 (CDC 1400-74)	USA (Rezzonico et al., 2009)	Human (ear)	Clinical isolate	-	-
ATCC 27998 (CDC 1741-71)	USA (Rezzonico et al., 2009)	Human (trachea)	Clinical isolate	-	-
EM 21cb	Spain (Rezzonico et al., 2009)	Human (bile)	Clinical isolate	-	-
EM 22cb	Spain (Rezzonico et al., 2009)	Human (blood)	Clinical isolate	-	-
LMG 1286^{T}	Zimbabwe (Rezzonico et al., 2009)	Human (knee wound)	Clinical isolate	-	-
VA21971	Spain (Rezzonico et al., 2009)	Human (arm wound)	Clinical isolate	-	-
CIP 82.100	Canada (Rezzonico et al., 2009)	*Triticum aestivum* (wheat)	Environmental	-	-
LMG 2557	United Kingdom (Rezzonico et al., 2009)	*P. communis*	Environmental	-	-
LMG 2595	South Africa (Rezzonico et al., 2009)	*Allium cepa* (onion, necrotic stalk/leaf)	Environmental	-	-
LMG 2941	N/A (Rezzonico et al., 2009)	*Malus sylvestris* (leaf, epiphyte)	Environmental	-	-
P3SA	Australia (Rezzonico et al., 2009)	*T. aestivum* (rhizosphere)	Environmental	-	-
P. agglomerans pv. *gypsophilae*					
ATCC 43348	USA (Rezzonico et al., 2009)	*Gypsophila paniculata* (baby's breath, plant gall)	Phytopathogen	-	-

CFBP 4342	The Netherlands (Rezzonico et al., 2009)	*G. paniculata* (plant gall)	Phytopathogen	-	-
Pantoea sp.					
Eh252	USA (44)	*Malus pumila*	Biocontrol agent	+	-
EPS486	Spain (Rezzonico et al., 2009)	*M. x domestica*(bud)	Environmental	-	-
EPS595	Spain (Rezzonico et al., 2009)	*P. communis* (bud)	Environmental	-	-
Pantoea septica					
LMG 5345	USA (Rezzonico et al., 2009)	Human	Clinical isolate	-	-
Pantoea brenneri					
ATCC 29001 (CDC 164-75)	USA (Rezzonico et al., 2009)	Human (prostate)	Clinical isolate	-	-
LMG 5343^{T}	USA (Rezzonico et al., 2009)	Human (urethra)	Clinical isolate	-	-
Pantoea dispersa					
CIP 102701	France (Rezzonico et al., 2009)	Human (ear)	Clinical isolate	-	-
LMG 2770	USA (Rezzonico et al., 2009)	Human (blood)	Clinical isolate	-	-
LMG 2603^{T}	Japan (Rezzonico et al., 2009)	Soil	Environmental	-	-
LMG 2605	Tanzania (Rezzonico et al., 2009)	*Vigna unguiculata* (cow pea, seed)	Environmental	-	-
Pantoea ananatis					
ATCC 27995 (CDC 4854-73)	USA (Rezzonico et al., 2009)	Human	Clinical isolate	-	-
LMG 5342	USA (Rezzonico et al., 2009)	Human	Clinical isolate	-	-
ATCC 27996	USA (Rezzonico et al., 2009)	Insect	Environmental	-	-
LMG 20103	South Africa (Rezzonico et al., 2009)	*Eucalyptus* sp.	Phytopathogen	-	-
LMG 2665^{T}	Brazil (Rezzonico et al., 2009)	*Ananas comosus* (pineapple)	Phytopathogen	-	-
LMG 2676	USA (Rezzonico et al., 2009)	*Puccinia graminis* f.	Phytopathogen	-	-

		sp. *tritici* (cereal stem rust-black rust)			
Pantoea conspicua					
EM 17cb	Spain (Rezzonico et al., 2009)	Human (blood)	Clinical isolate	-	-
Pantoea stewartii subsp. *indologenes*					
CFBP 3614^{T}	India (Rezzonico et al., 2009)	*Setaria italica* (foxtail millet, leaf spot)	Phytopathogen	-	-
P. stewartii subsp. *stewartii*					
CFBP 3517^{T}	USA (Rezzonico et al., 2009)	*Zea mays* var. *rugosa* (maize, corn)	Phytopathogen	-	-
Erwinia oleae					
CFBP 6632^{T}	Spain (Rezzonico et al., 2009)	*Olea europaea* (olive, plant gall)	Phytopathogen	-	-
Enterobacter sp.					
LMG 5339	USA (Rezzonico et al., 2009)	*Gallus gallus* (chicken, liver)	Veterinary isolate	-	-
Tatumella citrea (ex. *Pantoea citrea*)					
LMG 23359	Philippines (Rezzonico et al., 2009)	*A. comosus*	Environmental	-	-
Tatumella punctata (ex. *Pantoea punctata*)					
LMG 22097	Japan (Rezzonico et al., 2009)	*Citrus* x *sinensis* (orange)	Environmental	-	-

We previously proposed (Smits et al., 2011) that this compound would be identical to dapdiamide E, but now we are referring to the compound as herbicolin I to be consistent with earlier publications (Ishimaru et al., 1988; Dawlaty et al., 2010) and because the stereochemistry for both compounds has not been determined.

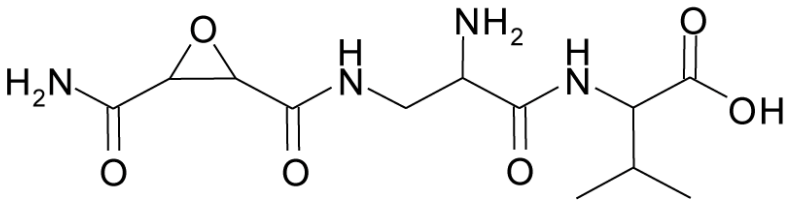

Figure. 1 Chemical structure of herbicolin I (2-amino-3-(oxirane-2,3-dicarboxamido)-propanoyl-valine).

Identification of the herbicolin I gene cluster

To identify the herbicolin I biosynthetic genes, a pTn*Mod* –RKm' plasposon mutant library of *P. vagans* C9-1 was constructed. This library, consisting of 3,800 plasposon mutants, was screened for the loss of antibiotic production in a double agar diffusion assay using the pantocin A-resistant and dapdiamide (herbicolin I)-sensitive biosensor strain CIR555. A total of 38 mutants were potentially deficient in dapdiamide biosynthesis. The flanking regions of all mutants were sequenced and analyzed using the BLASTN subroutine of GenDB (Meyer et al., 2003) against the fully annotated genome sequence of *P. vagans* C9-1 (Smits et al., 2011). A total of 25 plasposon insertions were located in a single locus that was identified as the biosynthetic operon of herbicolin I (Table 3). The operon consists of 10 genes (*ddaA-ddaI*) (Fig. 2) and is located on plasmid pPag2 in a region with a lower G+C content compared to the overall G+C content of the plasmid. This indicates that *P. vagans* C9-1 acquired herbicolin I biosynthesis most probably by horizontal gene transfer. However, immediately flanking the operon, no direct evidence for transposition could be found, so this cluster may have been acquired together with the complete plasmid pPag2, which is described as a biocontrol-specific feature (Smits et al., 2011). The other plasposon insertions are infrequently distributed on the chromosome and the other plasmids pPag1 and pPag3 and are most likely not involved in the biosynthesis of herbicolin I. The most frequent insertion sites of the plasposons were identified in *ddaB*, *ddaF1*, *ddaG*, and *ddaI*. DdaB is predicted to be involved in L-2,3-diaminopropionic acid (DAP) biosynthesis, one of the central monomers

linked to valine and fumaramic acid via condensation reactions by DdaF and DdaG to form the dapdiamide (Hollenhorst et al., 2009). DdaI is predicted to be involved in export of the antibiotics. The gene products of *ddaB*, *ddaF1*, *ddaG*, and *ddaI* appear to be strictly required for herbicolin I biosynthesis. We identified only few or none plasposon integration in the genes *ddaCDE* and *ddaH*. In studies of genes cloned from *P. agglomerans* CU0119 and expressed in *E. coli*, *ddaH* and *ddaCDE* are involved in the biosynthesis of the fumaramic acid moiety and formation of the epoxide precursor of N_{β}-epoxysuccinamoyl-DAP, respectively (Hollenhorst et al., 2011). One mutant identified as containing a plasposon insertion in the putative self-resistance gene *ddaI* produced less antibiotic than wild type and remained viable on the antibiotic production medium, MGA.

Table 3 Plasposon Tn*Mod*-RKm' mutant insertion identification

C9-1 plasposon mutant	Locus tag	Gene	Putative function
CIR620, CIR621, CIR625, CIR635, CIR646	Pvag_pPag20158	*ddaB*	Ornithine cyclodeaminase
CIR613	Pvag_pPag20159	*ddaC*	Fe(II)/α-KG-dependent dioxygenase
CIR591, CIR603, CIR619, CIR633	Pvag_pPag20162	*ddaF1*	Biotin carboxylase
CIR624	Pvag_pPag20163	*ddaF2*	Biotin carboxylase
CIR592, CIR594, CIR596, CIR597, CIR600, CIR616, CIR617, CIR626	Pvag_pPag20164	*ddaG*	Phenylacetate-CoA ligase
CIR599	Pvag_pPag20165	*ddaH*	Asparagine synthetase
CIR589, CIR614, CIR636, CIR641	Pvag_pPag20166	*ddaI*	Putative membrane protein

P. vagans C9-1 significantly reduced the incidence of disease symptoms on immature pear fruits inoculated with *E. amylovora* Ea110 at each time point compared to the buffer treatment (Fig. 3). Biocontrol was significantly decreased with *P. vagans* C9-1 Tn*Mod* mutants lacking production of herbicolin I (CIR591) or pantocin A (CIR638) compared to the wild type (Fig. 3). The mutant lacking production of herbicolin I and pantocin A (CIR600) did not suppress symptoms and the incidence of disease was similar to treatment with buffer (Fig. 3). All mutants were unaltered in growth rates compared to the wild type (data not shown) and each showed reduced biocontrol activity even when applied at 5 X 10^6 cfu ml^{-1} (Fig. 3A).

Among 59 isolates of the pathogen *E. amylovora* from commercial orchards, two isolates were tolerant of herbicolin I in the double diffusion agar assay, but sensitive to the histidine-reversible antibiotic pantocin A. These two orchard isolates had a similar inhibition pattern as the herbicolin I-resistant biosensor CIR550 with an inhibition zone distal from the *P. vagans* C9-1 colony, which was abolished when histidine was added to the overlay medium. One of the herbicolin I-tolerant isolates was resistant to 100 μg ml^{-1} streptomycin and the other was sensitive; both caused necrosis and production of bacterial ooze in immature pear fruits. All of the isolates of strain Ea153 recovered from diseased blossom clusters on inoculated trees treated with *P. vagans* C9-1 were sensitive to both herbicolin I and pantocin A.

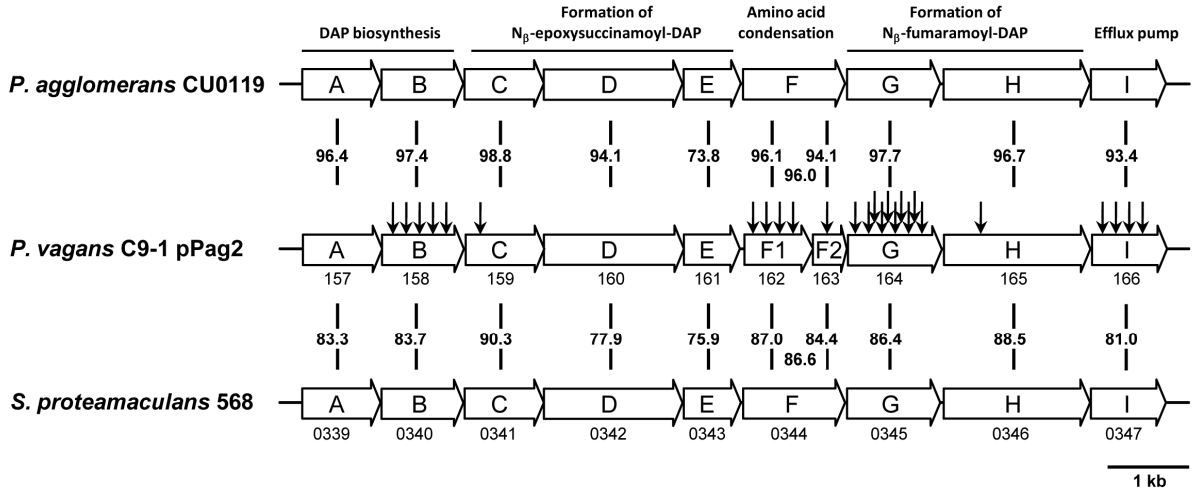

Figure 2 Dapdiamide operon of *Pantoea vagans* C9-1, *P. agglomerans* CU0119, and *S. proteamaculans* 568. The proposed biochemical functions encoded by the genes of *P. agglomerans* CU0119 (16) are indicated above. Plasposon insertion sites are indicated by arrows. Numbers between clusters indicate the identity on amino acid level. Where available, locus tags are indicated directly below clusters: for *P. vagans* strain C9-1 the prefix is Pvag_pPag20 and for *S. proteamaculans* strain 568 it is Spro_. Note that the gene cluster of *P. vagans* C9-1 differs in the number of genes due to the naturally separated genes *ddaF1* and *ddaF2*, which together constitute the biochemical function of *ddaF* in *P. agglomerans* CU0119.

Sequence analysis

BLAST search (NCBI) revealed the presence of highly similar gene clusters in the genomes of *P. agglomerans* CU0119 (Dawlaty et al., 2010), *Serratia proteamaculans* 568 (Taghavi et al., 2009) and a distantly related gene cluster in *Vibrio caribbeanicus* ATCC BAA-2122 (Hoffmann et al., 2012). The sequence of the gene cluster of *P. agglomerans* 48b/90 is not available, but the operon structure of *P. agglomerans* CU0119 (Dawlaty et al., 2010) is very similar to *P. vagans* C9-1 (Fig. 2). The gene cluster of *P. agglomerans* CU0119 has been

cloned and expressed in *E. coli* and shown to produce a mixture of dapdiamides (Dawlaty et al., 2010). As the sequence of *P. agglomerans* CU0119 (Dawlaty et al., 2010) only comprises the dapdiamide biosynthesis cluster, no evidence for horizontal transfer to *P. agglomerans* CU0119 is available.

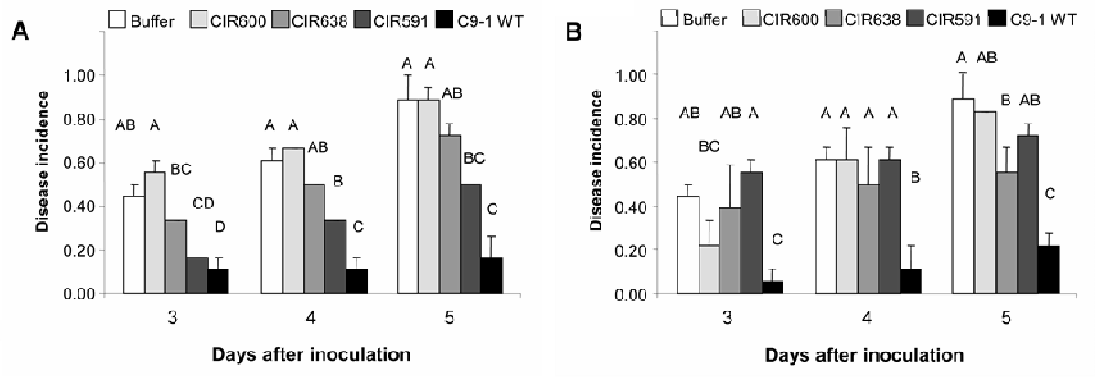

Figure 3. Reduction of incidence of disease symptoms (necrosis and/or bacterial ooze) in immature pear fruit by *P. vagans* C9-1 and antibiotic deficient derivatives CIR591 (herbicolin I^-/pantocin A^+), CIR638 (herbicolin I^+/pantocin A^-), and CIR600 (herbicolin I^-/pantocin A^-). Immature pear fruits were treated with (**A**) buffer or 5 $X10^6$ cfu ml^{-1} wild type C9-1 or derivatives or (**B**) buffer or 5 X 10^5 cfu ml^{-1} of wild type C9-1 or antibiotic deficient mutants, and subsequently challenged with 5 $X10^5$ cfu ml^{-1} *E. amylovora* Ea110. Vertical lines indicate standard error of the mean. Similar letters above bars for a time point indicate that the transformed incidence of symptoms between treatments is not significantly different according to Fisher's protected least significant difference at P =0.05.

In comparison to 10 genes in *P. vagans* C9-1, the clusters of *P. agglomerans* CU0119 and *S. proteamaculans* 568 consists of nine genes. Overall the gene cluster is highly conserved between *P. vagans* C9-1 and *P. agglomerans* CU0119 (above 90% amino acid identity), except for *ddaE* (Pvag_pPag20161) (73.8% identity). In the two other strains, the genes *ddaF1* and *ddaF2* are combined to only one ORF, a homolog of biotin carboxylase functioning in the condensation reaction between N_β-fumaramoyl-DAP and valine (Hollenhorst et al., 2011). A putative insertion event of 6 bp led to amino acid changes in Pvag_pPag20162. The insertion resulted in a leucine instead of proline, an additional cysteine and an early stop codon in Pvag_pPag20162 compared to the other two strains. The bases integrated directly in front of a methionine codon, which serves as start codon for *ddaF2* (Pvag_pPag20163).

Screening for dapdiamide biosynthetic genes in *Pantoea* species

A broad collection of *Pantoea* spp. that includes biocontrol, clinical and environmental isolates (Rezzonico et al., 2009), was screened for the presence of the dapdiamide biosynthetic genes (Table 1). The collection was tested for the presence of dapdiamide biosynthetic genes using two different primer combinations targeting *ddaD* (Pvag _pPag20160) and *ddaF1/ddaF2* (Pvag _pPag162, Pvag _pPag20163). The primers were generated by comparison of the three available sequences (Fig. 1). The dapdiamide genes were detected only in *P. vagans* C9-1 and its non-pigmented variant C9-1W cured of its megaplasmid pPag3 (Smits et al., 2010a).

Disscussion

The establishment and antibiotic synthesis of antagonists in the floral court is critical for successful suppression of *E. amylovora* (Giddens et al., 2003). Biocontrol strains that either naturally produce no antibiotic or are inactivated in biosynthesis of an antibiotic can still reduce the growth of *E. amylovora* (Vanneste et al., 1992; Stockwell et al., 2002; Giddens et al., 2003). Antibiotic biosynthesis mutants inhibit the growth of the pathogen to a lesser extent than the producing strains, as site exclusion and competition for limited nutrients (e.g., nitrogen, iron) are still active. Recovered isolates of the pathogen inoculated to trees treated with the biocontrol agent were sensitive to both antibiotics produced by *P. vagans* C9-1. Among isolates of the pathogen from commercial pear orchards, 3% were resistant to herbicolin I, and all were sensitive to pantocin A. None of the commercial orchards in the Pacific Northwest, USA were exposed to *P. vagans* C9-1, which was isolated in Michigan, so the herbicolin I resistance was not correlated to exposure or selection pressure from this biocontrol agent. In double diffusion assays, spontaneous mutants of *E. amylovora* may arise over time that are resistant to herbicolin I or pantocin A; this was the source of the biosensor strains (Ishimaru et al., 1988). We anticipate that a low incidence of spontaneous mutation may lead to isolates of the pathogen with resistance to herbicolin I. Nonetheless, we postulate that *P. vagans* C9-1 would continue to be an effective management tool for fire blight, even if some strains of the pathogen were resistant to herbicolin I. *P. vagans* C9-1 produces another antibiotic pantocin A and the isolates insensitive to herbicolin I were sensitive to pantocin A, an antibiotic demonstrated to contribute to biocontrol efficacy (Vanneste et al., 1992; Wright et al., 2001; Stockwell et al., 2002). Along with antibiosis, *P. vagans* C9-1 effectively competes with the pathogen for floral nutrients and colonization sites. The multi-prong

approach of *P. vagans* C9-1 to colonize and secure niches on flowers likely will mitigate a 'breakdown' in biological control efficacy due to herbicolin I-resistant populations of the pathogen (Duffy et al., 2003).

P. vagans C9-1 produces at least two antibiotics in culture that suppress growth of *E. amylovora* (Ishimaru et al., 1988). One antibiotic of *P. vagans* C9-1 is suppressed by histidine and presumed to be pantocin A based on the presence of a pantocin A gene cluster in the genome and preliminary characterization of the antibiotic (Smits et al., 2010d; Smits et al., 2011). In our *Pantoea* collection, the presence of pantocin A producers is much lower than in a previous report indicating 61 of 88 *P. agglomerans* strains that produced a histidine-suppressible antibiotic were positive for pantocin A biosynthesis genes (Jin et al., 2003; Rezzonico et al., 2009). The other, herbicolin I was shown here to belong to the dapdiamide family of antibiotics. The most abundant histidine-insensitive antibiotic isolated from *P. vagans* C9-1 is the epoxide of dapdiamide A, N_{β}-epoxysuccinamoyl-DAP-valine, which has been synthesized and shown to be biologically-active against *E. amylovora* (Hollenhorst et al., 2011). The ^{1}H-NMR spectrum of the purified antibiotic was identical to that of 2-amino-3-(oxirane-2,3-dicarboxamido)-propanoyl-valine identified in *P. agglomerans* 48b/90, which has the same $[M+H]^{+}$ and biochemical properties as the isolated antibiotic (Sammer et al., 2009). These findings are consistent with the detection of 2-amino-3-(oxirane-2,3-dicarboxamido)-propanoyl-valine in culture filtrates of *P. vagans* C9-1 (34) by LC-ESI-MS. Based on recent studies with dapdiamides and synthesized dapdiamide analogues, dapdiamides target cell wall biosynthesis by attacking glucosamine-6-phosphate synthase (Hollenhorst et al., 2011).

Given the similarities between the biosynthetic gene clusters in *P. vagans* C9-1 and *P. agglomerans* CU0119, the antibiotic produced by the gene cluster in *P. vagans* C9-1 most likely uses a similar biosynthetic pathway. The biosynthesis of the dapdiamide antibiotics comprises the linkage of L-2,3-diaminopropionic acid (DAP) to two variable units (e.g., amino acids, fumaramic acid and derivates) via amide bond formation (Dawlaty et al., 2010; Hollenhorst et al., 2010). Culture supernatants of *E. coli* expressing the dapdiamide biosynthetic cluster from *P. agglomerans* CU0119 contained dapdiamide A as well as the less abundant variants dapdiamide B and C having an isoleucine or leucine moiety instead of valine. Dapdiamide D and dapdiamide E also were present. These differ in linkage of DAP to fumaramic acid and an epoxide instead of the fumaramic acid double bond, respectively (Dawlaty et al., 2010; Hollenhorst et al., 2010). It is possible that *P. vagans* C9-1 produces other dapdiamides that were not detected or isolated by the protocols used for isolation of N_{β}-

epoxysuccinamoyl-DAP-valine. For example, another histidine-insensitive antibiotic produced with the same antimicrobial activity spectrum as herbicolin I was detected in cultures of *P. vagans* C9-1, but due to low yield was not characterized further. Further studies on optimization of dapdiamide production and isolation from *P. vagans* C9-1 would be valuable in this respect and in future studies on the importance of N_{β}-epoxysuccinamoyl-DAP-valine or other dapdiamides in the biological control of fire blight by *P. vagans* C9-1.

DdaI, a putative membrane protein potentially involved in the export of the antibiotic, conferred resistance to sensitive *E. coli* to dapdiamide A (Dawlaty et al., 2010). In our screen, mutants with an integrated plasposon in this gene resulted in viable cells, which formed a reduced zone of inhibition to *E. amylovora*. This suggests that different mechanisms of self-resistance exist within *P. vagans* C9-1, as the mutation in the putative exporter does not lead to lethality caused by the intracellular accumulation of dapdiamides. The putative target, glucosamine-6-phosphate synthase, might be insensitive to dapdiamide due to enzymatic or steric protection. Alternatively, the antibiotic might not be activated before its export, therefore displaying no toxic effect on the cells. However, additional mutagenesis and complementation studies would be required to determine the function of *ddaI* in *P. vagans* C9-1.

Biosynthesis of dapdiamide antibiotics is not a common trait in *Pantoea* spp. We identified dapdiamide biosynthetic genes only in *P. vagans* C9-1 and *P. agglomerans* CU0119 after screening a wide range of biocontrol, environmental, and clinical isolates. The rarity of dapdiamide biosynthesis within *Pantoea* spp. suggests that pathogen inhibitory activity described for biocontrol *Pantoea* strains is likely due to production of other antibiotic compounds (Rezzonico et al., 2007; Pusey et al., 2011). Analysis of the genes revealed that the operon, consistent of nine CDS in *P. agglomerans* CU0119 (Dawlaty et al., 2010), has 10 CDS due to base insertions in *P. vagans* C9-1. Besides this, the clusters have a similar gene organization and the gene products display high similarity on amino acid level to *S. proteamaculans* 568 (Fig. 2). Another member of this genus, *Serratia plymuthica*, also was described to produce a dapdiamide compound (Shoji et al., 1989; Sammer et al., 2009). Notably, N_{β}-epoxysuccinamoyl-DAP-valine was not isolated from culture supernatants of *E. coli* expressing the dapdiamide genes from *P. agglomerans* CU0119. Although the genes and predicted proteins share a high degree of similarity, differences in dapdiamide production between *P. agglomerans* CU0119 and wild type *P. vagans* C9-1 might reflect slight genetic differences between dapdiamide structural genes or its regulation. It is also possible that sequences outside of the dapdiamide gene cluster affect the composition of dapdiamide

antibiotics produced. We identified several plasposon mutants containing insertions outside the biosynthetic cluster that were deficient or reduced in herbicolin I. Methods used to purify dapdiamide antibiotics also may have influenced the types of dapdiamides detected.

The operon is most likely acquired by horizontal gene transfer, which is evidenced by the lower G+C content (47%) of the genes in both *Pantoea* strains than compared to the G+C content of the chromosome (53.8%; (Smits et al., 2011)). The dapdiamide biosynthesis operon is located on plasmid pPag2 that comprise diverse IS elements which indicates that many important biocontrol attributes of *P. vagans* C9-1 might be acquired traits (Smits et al., 2011). Sorbitol metabolism, indole acetic acid biosynthesis from aldoximes and tellurite resistance are located on this plasmid and might contribute to the ecological fitness of *P. vagans* C9-1. The biosynthesis of pantocin A and dapdiamide, as well as the overlapping nutrient utilization profile (Stockwell et al., 2010; Smits et al., 2011) of *P. vagans* C9-1, contribute to the effectiveness of this biocontrol agent to inhibit the growth of *E. amylovora*.

Confirmation of the chemistry and genetics of this biocontrol trait in C9-1 resolves outstanding regulatory questions regarding active-ingredient mechanisms of action. Identification of the biosynthetic genes of dapdiamide will facilitate streamlining the screening process for new biocontrol agents by rapid selection of environmental isolates that produce dapdiamide antibiotics and have higher potential for effective pathogen suppression (Rezzonico et al., 2007). The genetic characterization presented here also provides a foundation for discovery of novel compounds produced by similar pathways or by a subset of the biosynthetic genes using different substrates for synthesis.

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Chapter 5

The apple flower reactome in response to fire blight infection

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The apple flower reactome in response to fire blight infection

Abstract

The bacterial pathogen, *Erwinia amylovora*, is the causal agent of fire blight disease, a major disease threat to pome fruit production world-wide. The molecular basis of resistance and susceptibility are largely unknown. To assess the susceptible response of apple (*Malus* x *domestica*, variety 'Golden Delicious') to the fire blight pathogen the transcriptome of *E. amylovora* challenged and mock inoculated flowers obtained by RNA-sequencing was analyzed. A total of 67,958 transcripts are expressed at two day post inoculation, whereof 1,080 were differentially expressed (872 up and 208 down-regulated) in presence of the pathogen. The differentially expressed transcripts include putative disease resistance, stress, pathogen-related, general metabolic, phytohormone and -related genes. Reads that mapped to regions on the apple genome where no genes were assigned, could be used to identify potential novel genes. To identify transcripts specifically up or down-regulated in response to *E. amylovora* CFBP1430, we conducted RT-PCR using 28 differentially expressed transcripts as targets and compared the expression patterns to a biocontrol strain of *Pantoea vagans* C9-1, another apple pathogen *Pseudomonas syringae* pv. *Papulans papulans* FAW 388-01, and mock inoculated apple flowers.

Introduction

Plants have developed an arsenal of defense responses elicited by biotic and abiotic stresses. The specific recognition of pathogen effectors (Avr) by disease resistance (R) proteins leads to the induction of a hypersensitive response (local cell death) at the infection site and inhibition or growth stop of the pathogen. These activated responses are accompanied by induction of salicylic acid (SA) dependent signaling and expression of pathogen related proteins contributing to disease resistance. Cell wall reinforcement by callose and lignin deposition as physical barriers and phytotoxin production at the entry site of the pathogen represent a first line of defense. Defense responses against many necrotrophic pathogens are dependent on the combined accumulation and signaling of jasmonic acid (JA) and/or ethylene (ET) (Glazebrook, 2005). Beside this, JA and ET also control responses to wounding and various stresses (O'Donnell et al., 1996; Robert-Seilaniantz et al., 2011).

The apple genome of the fire blight susceptible varity 'Golden delicious' (*Malus* x *domestica* Borkh., family Rosaceae, tribe Pyreae) was recently sequenced and annotated (Velasco et al., 2010). The apple genome consists of 57,386 annotated genes with an

estimated size of 742.3 Mb. The genome sequence provides the basis for genetic, genomic, and transcriptomic analyses to gain insight to the apple biology.

The molecular basis of resistance and susceptibility of apple to *E. amylovora* is largely unknown. Until now no gene-for-gene interaction has been detected in the host-pathogen interaction. The infection process is accompanied by an oxidative burst in compatible and incompatible *E. amylovora*/ host plant interaction, indicating that the bacterium might exploit this pathway to invade host plant cells (Venisse et al., 2001). The hormone level of JA increased in the resistant cultivar Evereste compared to the susceptible MM106, whereas SA accumulates to the same extend in both conditions (De Bernonville et al., 2012). The lower accumulation of JA and down-regulation of the JA pathway might be an important step for successful infection of *Malus* spp. by *E. amylovora.*

Erwinia amylovora, an enterobacterial Gram-negative plant pathogen, is the causative agent of the fire blight disease, a major threat to pome fruit production world-wide, and with further impact on ecologically important cornerstone species. The pathogen infects plants mainly through the nectarthodes of flowers. Besides that, bacteria might get access through wounds caused by e.g., insect chewing or hail. Once in the host plant, it can spread through the vascular system throughout the whole plant. The multiplication of bacteria inside the vessels leads to their disruption causing the fire blight typical necrotic lesions in infected tissues. *E. amylovora* can provoke disease symptoms in fruits, shoots ("shepherd's crook") and rootstocks. Successful infection of susceptible host plant is dependent on secreted proteins from the bacterium by the hypersensitive response and pathogenicity (hrp) type III secretion system (T3SS). HrpN and the disease-specific, DspA/E, gene products are essential for virulence, since mutations in the encoding genes renders the pathogen less (Δ*hrpN*) or non-virulent (Δ*dspA/E*). DspA/E physically interacts with four serine/threonine receptor kinases of apple, designated as DspE-interacting proteins (Meng et al., 2006).

Previous studies used microarray, cDNA amplified fragment length polymorphism or suppression subtractive cDNA hybridization techniques to identify genes involved in the *E. amylovora–Malus* interaction (Norelli et al., 2009; Baldo et al., 2010; Sarowar et al., 2011). These studies gave first insights into this host-pathogen interaction, but are not reflecting the whole genome-wide transcriptional changes. RNA-sequencing was used to analyze the apple transcriptome of *E. amylovora* challenged flowers to gain further knowledge of the susceptible responses. 1,080 differentially expressed genes were detected 48 h post-inoculation, including genes of the jasmonic, ethylene and phenylpropanoid pathway.

Additionally, previously unknown genes in the apple genome could be assigned and unknown ORFs were detected in the genomes of *M. x domestica* and *Arabidopsis thaliana*.

Materials and Methods

Bacterial strains, media and growth conditions

The fire blight pathogen *Erwinia amylovora* CFBP1430 (Smits et al., 2010b), the biocontrol strain *Pantoea vagans* C9-1 (Smits et al., 2011) and the causal agent of blister spot *Pseudomonas syringae* pv. *papulans* FAW 388-01 were used for flower inoculations. The strains were plated on King's B (KB) medium from glycerol stocks kept at -86°C. Incubation temperature for all strains was 28°C. Inoculum and flower population sizes were determined on nutrient sucrose agar plates.

Flower inoculation

Freshly opened flowers of two year old 'Golden Delicious' plants, stored in a cold room, were either inoculated with 10 µl of a bacterial suspension (OD_{600}= 0.1, indicates approximately ~10^8 cfu ml^{-1}) or mock inoculated with water. The suspension was directly applied to the hypanthium with a pipette, not touching nor damaging plant organs. The flowering trees were kept at 20°C day and 18°C night with a relative humidity of 80%. Flowers were collected 48 h post inoculation. The flowers were cut with scissors, removing most of the peduncles. The petals were removed and the remainder parts were flash frozen in liquid nitrogen and then kept at -86°C until RNA extraction.

RNA extraction

Flowers were grinded in liquid nitrogen using RNAse-free pestles and mortars (incubated at 200°C overnight). Total RNA from flowers was isolated using the innuPREP Plant RNA Kit (Analytikjena, Germany) according to the manufacturer's instructions. Total RNA were treated with DNase I (Thermo Scientific, Switzerland) and control PCRs were performed to check for DNA contamination. Quality and concentration of the RNA samples were determined using the Bioanalyzer 2100 (Agilent Technologies, Germany). Samples were pooled to the required amount for further processing.

RNA-sequencing

cDNA libraries were prepared by Vertis Biotechnologie AG (Freising, Germany) and sequenced on an Illumina HiSeq 2000 machine. From the total RNA samples polyA+ RNA was isolated, treated with tobacco acid pyrophosphatase (TAP), then a RNA oligonucleotide carrying the T7 RNA promotor sequence was ligated to the RNAs. First-strand cDNA synthesis with oligo(dT)-linker primer was performed and PCR amplified. The full-length cDNAs were ultrasound fragmented, end-repaired and purified using the Agencourt AMPure XP kit (Beckman Coulter Genomics). TruSeq sequencing adapters were ligated to the cDNA fragments and PCR-amplified to about 20-30 ng/µl. A total of 3,549,589 and 12,839,290 (control, inoculated sample) 100bp reads were obtained from sequencing. The reads were screened for primer and polyA+ sequences leading to 1,991,992 and 6,138,188 filtered reads.

Data analysis

RNA-seq reads were mapped to the apple genome (Velasco et al., 2010) using TopHat version 2.0.0 (Trapnell et al., 2009) with bowtie version 0.12.7 (Langmead et al., 2009). Analysis of differential expression levels was performed using Cufflinks version 1.3.0 (Trapnell et al., 2010). Gene expression levels were normalized using the fragments per kilobase of exon per million mapped reads (FPKM) report values. To evaluate gene expression, four housekeeping genes coding for elongation factor 1 alpha subunit (MDP0000297959), importin alpha Isoform 9 (MDP0000126113), actin (MDP0000126113), and glyceraldehyde-3-phosphate dehydrogenase (MDP0000757565) were analyzed for significant diferential expression. None of these genes was significantly differentially expressed, meeting the requirements for further transcriptome analysis. Genes were considered as up- or down-regulated, when their fold change was ≥ 1.5 or ≤ -1.5, and their P value < 0.005.The underlying genomic sequences of read contigs that mapped to regions without assigned genes were extracted from the apple genome for further analysis. These sequences were used for BLAST analysis against *Arabidopsis thaliana* (Swarbreck et al., 2008) protein database 10 (TAIR10) to cover previously undetected coding sequences and to screen for novel ORFs in *A. thaliana* and *M. x domestica*. GO annotations were retrieved from http://www.rosaceae.org and used as input to create figures with the software WEGO (http://wego.genomics.org.cn/cgi-bin/wego/index.pl) (Ye et al., 2006).

cDNA construction and RT-PCR

The RevertAid H Minus First Strand cDNA Synthesis Kit (Thermo scientific, Switzerland) was used to construct cDNA from RNA samples. 1 µg of RNA was reversed transcribed with random hexamers according to the manufacturer's instructions and used for subsequent PCR. RT-PCR was performed with primer pairs listed in Table 1.

Results

Apple transcriptome analysis in response to *E. amylovora*

We inoculated apple flowers to investigate the susceptible response of the primary infection court of *E. amylovora*. Newly opened flowers were inoculated with a bacterial suspension or mock inoculated with water and collected 48 hours post inoculation, where the pathogen is fully established on the plant. Disease symptoms were not visible at the stage of sampling. Total RNA was isolated from flowers cleared from petals, rRNAs were depleted and subsequently the cDNA libraries were constructed for sequencing. A total number of 1,991,992 and 6,138,188 (control, inoculated) of reads were used for mapping, thereof 47.10% and 47.50% could be aligned to the apple genome sequence. The reads mapped to 63,508 annotated genes and 2,064 unnanotated regions in the apple genome sequence. Analysis of the mapped reads showed that the infection of *E. amylovora* led to significant differential expression of 1,080 apple transcripts, 208 are down- and 872 are up-regulated (Fig. 1, appendix Table 3).

The differentially expressed transcripts were assigned to cellular component, biological processes and molecular function according to the gene ontologies (GO) (Fig. 2). The main biological processes include response to stimulus, pigmentation, metabolic process, localization, establishment of localization, cellular process, and biological regulation.

Of the differentially expressed transcripts, 840 showed homology to annotated apple genes. However, 240 (217 up and 23 down-regulated) mapped to regions where previously no open reading frames (ORFs) were annotated. The sequences of these 240 novel transcripts were extracted from the apple genome sequence and a BLASTX analysis against *Arabidopsis thaliana* peptide database (TAIR 10) was performed resulting in 84 showing homology to *A. thaliana* proteins (suppl. Table 4, see appendix).

Table 1 Primer used in this study

Target	Forward primer sequence (5'–3')	Reverse Primer Sequence (5'–3')	Amplicon size (bp)	Annealing Temp (°C)
MDP0000293143	CGACTTTTAATTGGCCGTCA	AGGTGAACTCGGATTCCATC	139	-
MDP0000246508	ACTCCCTCGAAAATTCCTTC	GGGTACTACAGATGTGCCTT	204	53
MDP0000233439	GAGAAGCAGACGAGACCAC	AGTTTCCAAGTGGACCCTCT	127	53
MDP0000509613	GACAAGAGACTACCCCCTTG	AGCAATTTCTAGTTCTAGATCAG	193	53
MDP0000292176	CACAGGAGGAAGAGGAGG	AAACTCAAGGACAACCCG	211	53
MDP0000341297	ATGCTGCCGAGTTTTTG	ATACGATAAACATCATTAAAATACAAA	163	53
MDP0000295823	CTCTCAGCCTGCTTCACATT	AGTGTCGAAAGCTCGCTCTC	359	-
MDP0000279516	ATGTAAGCAGATATGAGGGATG	ATGGACCAGATGGAGATGA	312	-
MDP0000243237	CCTTTTGTAGTGGCTGACCT	CGAGTATCAATCCTAACAAAGC	167	53
MDP0000803538	TGGCAAGGCTACAATGGAG	GCAGACGAAGCAACGCA	458	53
MDP0000515106	TTCCTTGGCAAATCAGATTG	AGCAAAGGCTTCTTCCACCT	640	53
MDP0000343634	GGTTCAAACAGGGGAGCA	TTCTGAAACAAGCCACAACA	141	53
MDP0000314223	TATCCTAGGTGGGGCGTGGT	GCTGGTGCTTGTGGACGAAT	253	-
MDP0000850409	CTACTCACGGAGATGGGAA	GAACGTGAATGTTGGGTTG	196	53
MDP0000364657	GAGGCAATGAAGATGAACC	CACATACAACTCCATCAACAA	241	53
MDP0000201700	CCCTCGCTACTTCACCATA	CCTTGTCGTTCTTCTTGTCC	180	53
MDP0000361511	GATGGTGGAGGCAGTACAA	TACCCAACTCTCTGGAGAGTT	297	53
MDP0000336695	CATCAAGCTCAATGTCCTCA	CAAGAAGCTCATAGTGCCTC	177	53

MDP0000361876	GCTTTCGATCATTTCACCTA	ACCGTCCGATGACATATAGA	177	53
MDP0000248516	GGAGACTTCCTTGCCTCAT	AGCTTTGGTACATTTTCGG	321	53
MDC015146.108: 31720-32772	TCTGACCATCCTGAGGTAAG	GAAAGACAGTGCCTTCACAG	225	53
MDP0000297541	GTCGAGCGGCTCATCACA	GTCGTTACAATCATCGCCGT	148	53
MDP0000588940	TCGAGATGGGATATTGAAGG	TGGAGTAGGCTAGCCACATC	200	53
MDP0000511014	CCTTAGATCTCAGAAATTCAACCA	AGGCAACGGAGGCAATGT	239	53
MDP0000292511	TGATGCACCGTAAAACCAAG	CAATTATGCCACCACCACA	384	53
MDP0000921319	AAGGACACATGCCCCATT	CACAAGTGACAAGGAGCTGA	226	53
MDP0000294034	GGGCGGTTATACCTCATTC	GAGCTCCATCTCCATCTAAATC	272	57
MDP0000268505	CTGATAGGCCCAAAGACAAC	GTGGCACTGCGTAATGGTA	189	53
MDP0000412490	CACCCTCTCGACCATCTC	CCAATGTGTCGATGTCATAGTT	211	53
MDP0000757565	ATTGGTGACAGCAGGTCAA	AGAGGGTGGATGCTACGTG	148	53/57

These include transcripts with similarities to 1-aminocyclopropane-1-carboxylate (ACC) synthase, glutathione transferases, disease resistance and putative pathogenesis-related genes. Similar analysis was repeated for all unassigned transcripts of the transcriptome and yielded 749 BLAST hits (suppl. Table 5, see appendix).

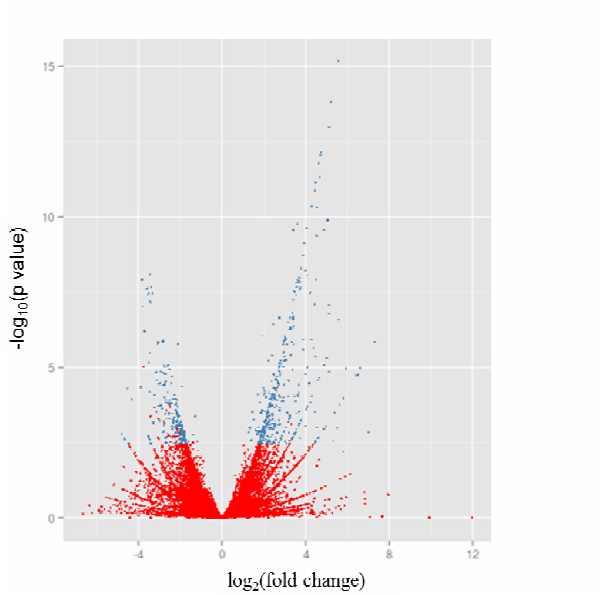

Figure 1 Volcano plot representing all expressed transcripts. For every transcript, the fold change of control compared to inoculated plant was plotted against the –log p value. The 1080 statistically significant differentially expressed genes ($p < 0.005$) with a fold change > 2 are depicted as blue, insignificant as red dots. A total number of 872 have higher and 208 lower transcript abundance in the inoculated compared to the control samples.

The 156 sequences which did not yield a significant BLAST hit at the protein level were used in BLASTN searches against the *A. thaliana* and *Prunus persica* genomes to identify possible conserved non-coding sequences or novel ORFs. None had DNA homology with *A. thaliana*, while 47 showed significant DNA homology to the (more closely related) *P. persica*. These were screened for DNA alignments in apple and *A. thaliana* sequences for base mismatches that are separated from each other by multiples of three. In protein coding sequences, the third position of the codon is more likely to differ, due to the degeneration of the genetic code. We identified 6 sequence alignments which were significantly enriched ($P < 0.05$) for such mismatch spacings. We conclude that these 6 sequences represent previously unknown ORFs specific to the *Malus*/*Prunus* lineage (Table 2). The other 41 transcripts which have DNA homology between *P. persica* and *M. x domestica* showed no evidence for coding capacity were classified as putative conserved non-coding sequences (CNS, Table 1). 109 of have no homologs in *P. persica* the transcripts are apparently specific for *M. x domestica*.

Differentially expressed genes

Genes generally related to response to biotic and abiotic stimuli e.g., glutathione S-transferases (e.g., GSTU8, GSTU19), cytochromes (mainly P450), NAC domain containing proteins (e.g., ANAC083, ANAC002), and ubiquitin- hydrolases and proteases (e.g., BRIZ1, UBQ12, UBQ13) showed differential expression. The first three classes of genes are all up-regulated, whereas the ubiquitin-related class contains up- and down-regulated genes. Either group of identified gluthatione S-transferases and cytochromes include 3 novel transcripts (GSTU7,GSTU8, GSTU19 and CYP72A9, CYP72A14, CYP76C2).

The identified photosynthesis genes, encoding light harvesting complexes (e.g., LHCB2.2, LHCB4.2) and chlorophyll A/B binding proteins (CAB1, ELIP1) are all down-regulated. Processes affected during the infection of apple blossoms by *E. amylovora* include defense responses to bacteria and fungi reflected by the differential expression of potential disease resistance, leucine-rich repeat, phytohormones and chitinase genes. Marker genes for hormones JA and ET biosynthesis and signaling pathway are up-regulated. In addition to the probable ethylene biosynthesis genes 1-aminocyclopropane-1-carboxylate (ACO/ACC) and ethylene-forming enzyme (ACO), genes involved in ethylene perception and signaling are induced, e.g., ethylene responsive element binding factors (ATERF-), ethylene sensor (ETR2), and ethylene response factors (ATERF). One of the central genes in MeJA biosynthesis, jasmonic acid carboxyl methyltransferase (JMT), is not differentially expressed at the sampling time point, however genes potentially involved in JA signaling are induced (JAZ2, ATMYC2/JIN1). Transcripts of JAR1 described as responsible for conversion of jasmonate to its active isoleucine form were either not detected or only at low, insignificant levels in the control and in the challenged datasets. Genes involved in the phenylpropanoid and flavonoid biosynthesis are induced indicated by the expression of the phenylalanine ammonia lyase (PAL) and various chalcone synthases (CHS).

Transcripts potentially involved in either direct or indirect perception and signaling of pathogens and wounding are differentially expressed (e.g., LOX2, RBOHD, MAPKKK4/19, NHL genes). Although we analyzed a susceptible host-pathogen interaction we detected putative disease resistance genes of the TIR-NBS-LRR and CC-NBS-LRR classes, receptor like kinases, WRKY transcription factors (e.g., WRKY33, WRKY40) and pathogenesis-related genes (e.g., PR1, PR4, PR5, PR8). All WRKY transcription factors, putative resistance genes, and PR show higher transcript abundance in the infected plant than in the water control.

Table 2 Potentially new open reading frames

Contig	Position	Length (bp)	Significantly differentially expressed
MDC003508.304	714-802	88	Yes
MDC004050.111	2972-3698	726	Yes
MDC006793.328	2502-2994	492	Yes
MDC006793.328	4674-5465	791	Yes
MDC017405.92	18343-18890	547	Yes
MDC019296.227	19299-19915	616	Yes
MDC000413.352	3148-3647	499	No
MDC002798.542	1811-2138	327	No
MDC003592.155	55-665	610	No
MDC005235.134	1103-1716	613	No
MDC005383.384	11599-12036	437	No
MDC005832.257	6368-6874	506	No
MDC009600.163	10216-10538	322	No
MDC009649.545	17049-17355	306	No
MDC010328.213	17735-18163	428	No
MDC010474.345	1721-2322	601	No
MDC010692.100	15414-15558	144	No
MDC010926.52	6566-6802	236	No
MDC011638.223	6587-6937	350	No
MDC012232.278	12728-13210	482	No
MDC012594.480	397-686	289	No
MDC013437.191	6984-7656	672	No
MDC014100.85	297-668	371	No
MDC016529.125	25569-25918	349	No
MDC017428.71	19752-19979	227	No
MDC017676.268	21261-21536	275	No
MDC018139.149	19551-19623	72	No
MDC018302.132	703-1163	460	No
MDC020690.260	20149-20524	375	No
MDC038224.11	9262-9560	298	No
MDC041335.7	2001-2706	705	No

We identified five genes encoding for leucine-rich repeat (LRR) family proteins with lower transcript abundance in the *E. amylovora* inoculated samples. One of these LRR family proteins encoding gene, MDP0000207774, is identical to MxdRLP1-1 on amino acid level and a second, MDP0000392201 is largely similar but differs on the C terminus by being sixty amino acids longer in sequence. The third LRR family protein, MDP0000315498, is distantly related to RLP1 alleles. Based on the amino acid sequence MDP0000281307 is not related to RLP1s. MDP0000303781 is annotated as a LRR family protein but analysis of the amino acid sequence indicates that leucine-rich repeats are absent from the gene product and therefore is not considered to belong to LRR-proteins.

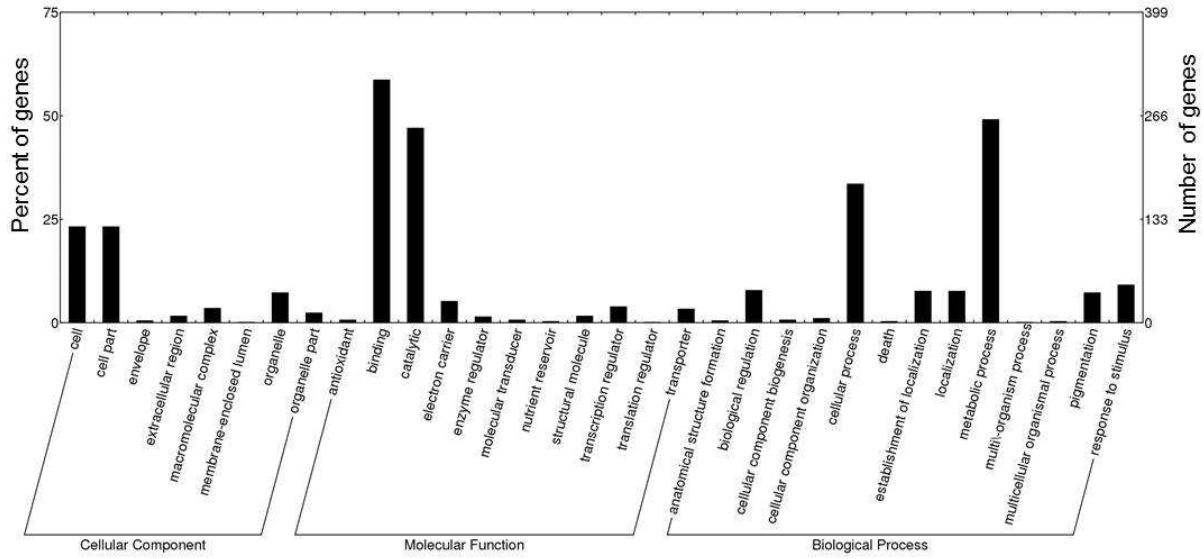

Figure 2 GO terms for the statistically differentially expressed apple genes in response to *E. amylovora* infection. Only the genes with GO terms are depicted.

Reverse transcription PCR (RT-PCR)

In order to assess if the transcriptional changes observed in the RNA-seq data, of apple in response to the *E. amylovora* infection process, were specific to the pathogen or common stress responses a RT-PCR was performed. *E. amylovora* CFBP1430 and *Pseudomonas syringae* pv. *papulans* FAW 388-01 were chosen to detect potential differences in apple response to pathogenic bacteria, *Pantoea vagans* C9-1 for influence of a biocontrol strain. Genes expressed in all bacteria inoculated flowers indicated a general reaction on these bacteria or stress response. Water inoculated flowers were used as control group. The flowers were inoculated with the bacterial strains or water and collected 48 h post inoculation for RNA extraction and subsequent cDNA reverse transcription. The RT-PCR was performed for

29 targets selected from differentially expressed transcripts (Table 3) from the RNA-seq data. Amplicons were obtained for 14 targets (Fig. 3) with varying band intensities for some of the genes tested in response to the different treatmensts. The gene MDP0000243237 was only expressed in the *P. syringae* pv. *papulans* FAW 388-01 and *Pantoea vagans* C9-1 inoculated samples. The gene is annotated as coding for a peroxidase superfamily protein.

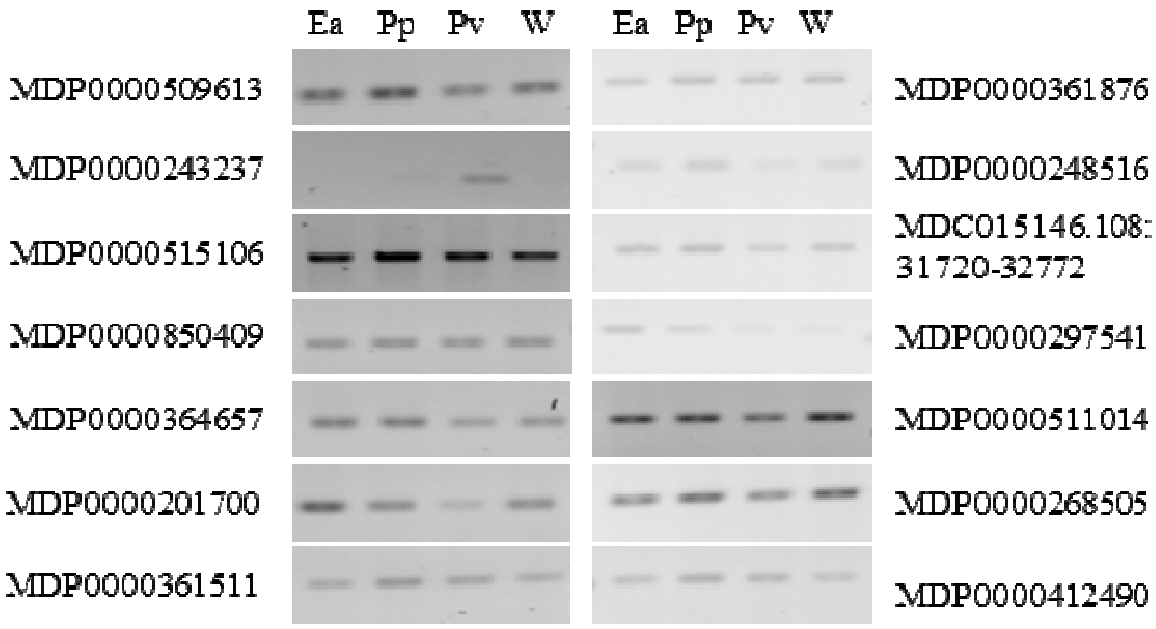

Figure 3 Expression patterns of selected genes in response to *E. amylovora* (Ea), *P. papulans* (Pp), *P. vagans* (Pv) and water (W) inoculation in apple flowers. The *M. x domestica* locus tags of the targets are indicated to the left right of corresponding gel panels.

Discovery of novel potential ORF and CNS

In total 1,088 transcripts that mapped to the apple genome did not correspond to annotated genes. Neither did they show homology at the protein level to *A. thaliana* proteins. To identify possible novel ORFs or CNS, we used these 1,088 sequences for BLASTN searches against the closely related *P. persica*. In total, 269 showed significant DNA homology (E-value < 10E-10) between *M. x domestica* and *P. persica*. Using the spacing between DNA mismatches as criteria (see above), we identified 25 putative new ORFs (table 2). We propose that these represent protein coding genes which are specific to the *M. x domestica*/*P. persica* lineage. The remaining 244, we consider to be potential CNS.

Table 3 Summary of RT-PCR results.

Target	*E. amylovora*	*P. papulans*	*P. vagans*	Water
MDP0000509613	+	+	+	+
MDP0000243237	-	+	+	-
MDP0000515106	+	+	+	+
MDP0000850409	+	+	+	+
MDP0000364657	+	+	+	+
MDP0000201700	+	+	+	+
MDP0000361511	+	+	+	+
MDP0000361876	+	+	+	+
MDP0000248516	+	+	+	+
MDC015146.108:31953-33995	+	+	+	+
MDP0000297541	+	+	+	+
MDP0000511014	+	+	+	+
MDP0000268505	+	+	+	+
MDP0000412490	+	+	+	+
MDP0000293143	na	na	na	na
MDP0000246508	na	na	na	na
MDP0000233439	na	na	na	na
MDP0000292176	na	na	na	na
MDP0000341297	na	na	na	na
MDP0000295823	na	na	na	na
MDP0000279516	na	na	na	na
MDP0000803538	na	na	na	na
MDP0000343634	na	na	na	na
MDP0000314223	na	na	na	na
MDP0000336695	na	na	na	na
MDP0000588940	na	na	na	na
MDP0000292511	na	na	na	na
MDP0000921319	na	na	na	na
MDP0000294034	na	na	na	na

Table 4 Targets for RT-PCR

Targets	*Arabidopsis*	Gene name/alternative name(s)	Full name
MDP0000343634			
MDP0000314223	AT1G78610.1	MSL6	mechanosensitive channel of small conductance-like 6
MDP0000850409			
MDP0000364657			
MDP0000201700	AT5G59845.1		Gibberellin-regulated family protein
MDP0000361511	AT3G22142.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000336695	AT4G39250.1	ATRL1,RL1,RSM2	RAD-like 1
MDP0000361876	AT4G03210.1	XTH9	xyloglucan endotransglucosylase/hydrolase 9
MDP0000248516	AT5G09530.1		hydroxyproline-rich glycoprotein family protein
MDC015146.108: 31720-32772	AT2G04780.2	FLA7	fasciclin-like arabinogalactan-protein 7 (Fla7)
MDP0000297541	AT4G10810.1		
MDP0000588940	AT3G27200.1		Cupredoxin superfamily protein
MDP0000511014			
MDP0000292511	AT1G31280.1	AGO2	Argonaute family protein
MDP0000921319	AT2G10940.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000294034	AT5G54490.1	PBP1	pinoid-binding protein 1
MDP0000268505	AT1G29980.1		Protein of unknown function, DUF642
MDP0000412490	AT1G56430.1	ATNAS4,NAS4	nicotianamine synthase 4
MDP0000293143	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000246508			
MDP0000233439	AT2G31955.1	CNX2	cofactor of nitrate reductase and xanthine dehydrogenase 2

MDP0000509613	AT5G54500.1	FQR1	flavodoxin-like quinone reductase 1
MDP0000292176	AT1G08450.1	AtCRT3,CRT3,EBS2,PSL1	calreticulin 3
MDP0000341297			
MDP0000295823	AT5G20040.1	ATIPT9,IPT9	isopentenyltransferase 9
MDP0000279516	AT2G18470.1	PERK4	proline-rich extensin-like receptor kinase 4
MDP0000243237	AT5G17820.1		Peroxidase superfamily protein
MDP0000803538	AT3G03940.1		Protein kinase family protein
MDP0000515106	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein

Discussion

The fire blight disease caused by *E. amylovora* is a world-wide threat for apple and pear production. RNA-sequencing provides a novel tool for transcriptional profiling and to discover previously undetected genes in the target genome. The recent publication of the complete apple genome sequence (Velasco et al., 2010) enabled us to study the transcriptional changes in apple blossom elicited by *E. amylovora* in its genetic background. RNA-sequencing is advantageous to other methods (e.g., microarray) used to analyze transcriptomes concerning nucleotide resolution and quantification of low abundant transcripts. In this study RNA-sequencing was applied to investigate the susceptible response of blossom of the economically important apple cultivar 'Golden delicious'. The transcriptome analysis not only led to the discovery of pathways and genes differentially expressed in response to *E. amylovora*, but as well uncovered novel genes and potential ORFs in apple and *Arabidopsis*. The BLASTX analysis of all unassigned transcripts of the apple transcriptome against the *A. thaliana* proteins yielded potential novel genes in the *M. x domestica* genome, but did not cover all transcripts. *A. thaliana* is commonly used as reference to annotate novel plant genomes, but might be insufficient to annotate all genes of distantly related plant species. Therefore we applied a comparative BLASTN approach, using the closely related species *P. persica* genome as reference, to identify potential ORFs. This method was more efficient by using the *P. persica* compared to *A. thaliana* genome and led to the identification of genes specific to the *Malus*/*Prunus* lineage.

Our results show that genes of the jasmonic acid pathway are differentially expressed after 48 hours post inoculation. It was recently reported that JA levels increase to much higher extend in apple leaves in the resistant cultivar 'Evereste' compared to the susceptible MM106 (De Bernonville et al., 2012). Treatment of the susceptible plants with methyl-jasmonate prior inoculation renders them more resistant to *E. amylovora* infection. We found that *jmt* and *jar1* are not differentially expressed in 'Golden delicious' flowers 48 hours post inoculation, but we identified genes of the jasmonic acid pathway that are significantly up-regulated. If this differential expression pattern leads to a differing accumulation of jasmonic acid in the infected cultivar 'Golden delicious' compared to a resistant one is not known.

ET -biosynthesis and -responsive genes are significantly induced. The up-regulation of these genes might be a direct response to *E. amylovora* or triggered by tissue damage and therefore a wounding/stress response. ET biosynthesis silenced apple fruits were shown to be more susceptible to the fungal pathogen *Botrytis cinerea* (Akagi et al., 2011). If a similar

effect of ET could be observed in the *E. amylovora* host plant interaction should be evaluated comparing susceptible and resistant plant under pathogen attack.

Phenylpropanoid pathway gene expression induction (e.g., phenylalanine ammonia lyase) indicates phytoalexin production, in the susceptible interaction of *E. amylovora* and apple. This is supported by the fact that phytoalexins accumulate in the transition zone (healthy-necrotic) of a susceptible apple cultivar (Chizzali et al., 2012). These phytoalexins show *in vitro* inhibitory effects against *E. amylovora* at elevated levels, however *in planta* the disease progress is not stopped but might be delayed. It is not known if the variety 'Golden delicious' challenged with *E. amylovora* synthesizes phytoalexins with an inhibitory effect.

The overexpression of the *npr1* gene (nonexpressor of PR 1) led to the activation of PR2, PR5, and PR8 and enhanced disease resistance to fire blight (Malnoy et al., 2007). Elevated levels of PR2 transcripts were only detected in *E. amylovora* inoculated plants overexpressing *npr1* leading to the assumption that the activation of this gene might be involved in disease resistance. We identified in the apple transcriptome PR1, PR4, PR5 and PR8 genes to be up-regulated, whereas PR2 is not differentially expressed. It has not been revealed if PR2 is activated and contributes to resistance in incompatible *E. amylovora* apple interactions.

Recently five genes encoding for leucine-rich repeat, receptor-like proteins were identified as putative fire blight resistance genes (MxdRLP1-1- MxdRLP1-5) (Gardiner et al., 2012). The allele MxdRLP1-2 was identified only in resistant cultivar R5, whereas the others were detected in resistant and susceptible *Malus* cultivars. Genes encoding leucine-rich repeat (LRR) family proteins were detected in our study. The gene MDP0000207774 is identical to MxdRLP1-1 and highly similar to MDP0000392201 on amino acid level apart of the C terminus. All leucine-rich repeat (LRR) family proteins have lower transcript abundance in the fire blight inoculated apple blossoms compared to the control. The MxdRLP1 alleles are candidate resistance genes, therefore genes encoding for LRR family proteins might be direct or indirect targets in the *E. amylovora – M. x domestica* 'Golden delicious' interaction in order to modulate host defense responses.

The observed down-regulation of photosynthesis genes is in accordance with observations in other pathosystems (Bonfig et al., 2006; Khalaf et al., 2011). The photosystems are a potential source of reactive oxygen species (ROS) that can induce defense responses and a hypersensitive response in incompatible interaction limiting pathogen growth. The opposing case occur in the compatible *E. amylovora* - host interaction, the pathogen seem to exploit ROS production to provoke cell death to invade plant tissues (Venisse et al., 2001).

The RT-PCR revealed that MDP0000243237 only was expressed in the *P. syringae* pv. *papulans* FAW 388-01 and *Pantoea vagans* C9-1 inoculated samples. In the RNA-seq data this gene was not expressed in the mock (FPKM value was 0) and only at a low level in the *E. amylovora* (FPKM value was 4.93) inoculated sample, which led to the assignment that the gene is significantly diffential expressed. This none and low level of expression might be under the detection limit for the RT-PCR of this gene in the *E. amylovora* and mock inoculated samples. Nevertheless, MDP0000243237 (annotated as coding for a peroxidase superfamily protein) is expressed in apple flowers in response to *P. syringae* pv. *papulans* FAW 388-01 and *Pantoea vagans* C9-1. Since this gene was lower expressed in the *E. amylovora* inoculated samples, it might be a target for modulation during the infection process.

The RT-PCR results indicated that specific apple responses to *E. amylovora* can be detected by comparing the gene expression patterns of the plant inoculated with different bacteria. The approach could be expanded to whole transcriptome analysis to identify candidate genes conferring resistance or susceptibility in a given cultivar. This might be advantageous to the comparison of cultivars with different genetic background by reducing the number genes to a common set

Upon *E. amylovora* attack apple elicits an array of defense responses, reflected in the expression of genes of the JA, ET, and phenylpropanoid pathways as well as putative resistance genes. Since we analyzed a compatible host-pathogen interaction the induction of these pathways do not limit disease progression. Either the pathogen modulates/delay the responses directly by secreted effectors or susceptible plants might not accumulate/produce inhibitory compounds to the level needed to stop pathogen growth.

Chapter 6

General conclusion and outlook

Conclusion

As fire blight is a recurrent threat for pome fruit production with further impact on ecological cornerstone species, effective control strategies are needed. The identification of the Achilles heel of the pathogen, mechanisms that contribute to the effectiveness of biocontrol agents and a profound understanding of the host-pathogen interaction, are required to develop such control measures. The transcriptomic and genomic approaches applied in this thesis enabled the identification of genes that potentially contribute to resistance/susceptibility of host plants, pathogen virulence and biocontrol features of biocontrol strains. The mutational analysis of the T6SSs in *E. amylvora* combined with the RNA-seq data indicated that these secretion systems affect metabolic processes and motility in host plants. The apple shoot and flower virulence assays as well as the *in vitro* transcriptome data suggested that the T6SSs have a minor contribution to the increase (shoots) and decrease (flowers) in virulence compared to the wild type strain. These opposing effects might thus be dependent on the environment.The analysis of mutants defective in herbicolin I biosynthesis led to the characterization of the antibiotic operon in *P. vagans* biocontrol strain C9-1. Herbicolin I biosynthesis contributes to the biocontrol effectivity of *P. vagans* C9-1 and was shown to be a rare trait in the screened *Pantoea* collection. The apple transcriptome data, revealed by RNA-seq, led to the identification of genes and pathways potentially involved in susceptibility of apple to *E. amylovora*. The data presented in this thesis provide a profound understanding of *M. x domestica* susceptible mechanisms, the T6SSs of *E. amylovora*, and the antibacterial peptide biosynthesis gene cluster in *P. vagans* C9-1. Based on this data, novel approaches may be developed to enhance resistance mechanisms in susceptible host plants as well as to facilitate the screening for novel biocontrol strains to protect flowers from *E. amylovora* infection.

Outlook

In this thesis, several aspects contributing to the virulence of *E. amylovora* were investigated. A new function of T6SSs (effect on motility) could be identified and future work will reveal if this is also the case in other bacterial species. Regarding the T6SSs in *E. amylovora,* additional functions could be discovered, as it is not a main virulence factor but influences metabolic and other virulence factors dependent on the environment (*in planta* versus *in vitro* transcriptome). Since the T6SS double mutant displayed differing phenotypes in the plant inoculation experiments, further long-term greenhouse plant assays could be performed to analyze effects on survival and canker development. These experiments should include an

artificial winter resting and a spring warming phase mimicking natural conditions. The apple RNA-seq transcriptome data revealed candidate genes and pathways that were affected by the infection of *E. amylovora* and thus could be involved in susceptibility. This could be confirmed by overexpressing or silencing these genes, namely those potentially involved in JA and ET signaling, the pathogenesis-related, and the putative disease resistance genes. The genetic information of the identified antibacterial peptide gene cluster of herbicolin I will facilitate streamlining the screening process for novel biocontrol agents by rapid selection of environmental isolates that produce this antibiotic.

Chapter 7

References

References

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Chapter 8

Appendix

Appendix

Table 1 All significantly differentially expressed transcripts from *in vitro* experiments comparing ΔT6SS-C1C3 to the *E. amylovora* wild type strain

gene	locus	T6SS-ΔD1ΔD3	WT	FPKM_1	FPKM_2	log2(fold_change)
EAMY_3011,EAMY_3012	NC_013961.1:3119097-3121730	M9	M9	219.93	516.959	1.23301
gph,rpe,trpS	NC_013961.1:3518602-3520971	M9	M9	705.848	1690.76	1.26025
EAMY_2488,cpxR3	NC_013961.1:2556450-2558492	M9	M9	173.202	436.807	1.33454
pdxY1,pdxY3	NC_013961.1:1770494-1771356	M9	M9	114.329	302.325	1.4029
EAMY_2193,yviA	NC_013961.1:2232024-2232868	M9	M9	484.258	1359.93	1.48968
hrcJ,hrpD,hrpE	NC_013961.1:618902-620852	M9	M9	266.511	748.729	1.49025
hrcC,hrpF,hrpG	NC_013961.1:620942-623608	M9	M9	677.938	1955.79	1.52853
EAMY_1066	NC_013961.1:1137155-1137398	M9	M9	1222.43	3531.79	1.53065
ygcM	NC_013961.1:836034-836394	M9	M9	343.314	1007.32	1.55293
livG,livH,livM	NC_013961.1:3582312-3585274	M9	M9	328.771	967.158	1.55667
yieE	NC_013961.1:3778734-3779478	M9	M9	116.66	343.485	1.55793
EAMY_0126	NC_013961.1:144754-145826	M9	M9	57.3203	168.843	1.55856
EAMY_0645	NC_013961.1:719905-720514	M9	M9	204.284	603.935	1.56382
znuB,znuC	NC_013961.1:2112113-2113650	M9	M9	159.107	472.989	1.57181
yhiN	NC_013961.1:3621757-3622942	M9	M9	76.9036	229.354	1.57645
yicG	NC_013961.1:78076-78694	M9	M9	83.6717	251.272	1.58644
mesJ	NC_013961.1:2823828-2825340	M9	M9	86.2815	259.502	1.58862
aaeB	NC_013961.1:348802-350761	M9	M9	37.1706	112.365	1.59596
spaI1,spaM1,spaN1,spaO1,spaP1,spaQ1	NC_013961.1:868966-873524	M9	M9	1429.4	4399.76	1.62202
EAMY_2276	NC_013961.1:2325474-2325897	M9	M9	200.51	623.994	1.63785
artJ	NC_013961.1:1380796-1381528	M9	M9	64.5155	204.207	1.66232
amsJ	NC_013961.1:2282961-2284209	M9	M9	128.497	409.017	1.67043
EAMY_0405,lcrS	NC_013961.1:469368-469717	M9	M9	423.3	1359.98	1.68383
EAMY_2957	NC_013961.1:3056602-3056932	M9	M9	325.44	1047.78	1.68688
EAMY_3631,dalD	NC_013961.1:3724495-3727328	M9	M9	280.55	907.437	1.69354
rpmG	NC_013961.1:103871-104039	M9	M9	4684.82	15223.2	1.70021
yneH	NC_013961.1:1857621-1858548	M9	M9	67.6892	222.127	1.71439

ybgR	NC_013961.1:1250689-1251619	M9	M9	108.212	358.109	1.72653
EAMY_1991	NC_013961.1:2054697-2054793	M9	M9	6021.89	20204.4	1.74638
mreC,mreD	NC_013961.1:337357-338865	M9	M9	248.378	838.875	1.75592
amiB,yjeE,yjeF	NC_013961.1:3249834-3253766	M9	M9	396.647	1339.96	1.75626
EAMY_2386,pta	NC_013961.1:2458566-2460911	M9	M9	313.501	1059.2	1.75643
ymcC	NC_013961.1:3445043-3445577	M9	M9	420.868	1433.77	1.76837
bolA	NC_013961.1:1058192-1058507	M9	M9	1640.55	5590.79	1.76887
sdaC	NC_013961.1:1368041-1369416	M9	M9	54.9471	187.696	1.77228
yhdZ	NC_013961.1:317406-318168	M9	M9	55.3087	195.878	1.82438
EAMY_3227	NC_013961.1:3323268-3324816	M9	M9	21.1313	75.1959	1.83127
EAMY_2092	NC_013961.1:2137243-2137622	M9	M9	179.5	639.928	1.83393
ychH	NC_013961.1:1667122-1667410	M9	M9	891.855	3218.3	1.85141
mod	NC_013961.1:938983-940450	M9	M9	118.545	429.737	1.85802
yddG	NC_013961.1:583485-584382	M9	M9	91.9707	334.55	1.86298
yhfC	NC_013961.1:3515659-3516844	M9	M9	85.4484	312.422	1.87037
ydcO	NC_013961.1:1592795-1594832	M9	M9	87.8334	321.485	1.87191
yrbE	NC_013961.1:382545-383328	M9	M9	147.728	546.583	1.88749
hsvA	NC_013961.1:597198-598299	M9	M9	157.372	583.461	1.89046
yjeR	NC_013961.1:3255005-3255587	M9	M9	139.04	515.804	1.89133
yeaZ	NC_013961.1:2065812-2066553	M9	M9	93.3671	346.729	1.89282
yebA	NC_013961.1:2109627-2111065	M9	M9	105.794	397.921	1.91122
ymcA,ymcB	NC_013961.1:3442198-3445008	M9	M9	193.504	742.709	1.94043
tolQ	NC_013961.1:1240742-1241420	M9	M9	227.618	874.308	1.94153
EAMY_2997	NC_013961.1:3096312-3096486	M9	M9	525.678	2020.94	1.94278
prtF	NC_013961.1:3667683-3669015	M9	M9	50.3289	193.807	1.94516
EAMY_3022	NC_013961.1:3126660-3127680	M9	M9	52.9032	204.874	1.95331
ycaD	NC_013961.1:1410345-1411497	M9	M9	206.066	802.432	1.96127
EAMY_0751	NC_013961.1:841283-841460	M9	M9	2453.39	9690.24	1.98176
EAMY_3271	NC_013961.1:3372550-3373090	M9	M9	72.3988	289.786	2.00095
EAMY_0010	NC_013961.1:21768-27714	M9	M9	64.5484	262.177	2.02209
flgM	NC_013961.1:1523187-1523487	M9	M9	606.69	2476.22	2.02911
plc	NC_013961.1:1826337-1827372	M9	M9	177.569	726.721	2.03302

norM	NC_013961.1:1748765-1750139	M9	M9	123.526	512.509	2.05277
ybiS	NC_013961.1:1296588-1297689	M9	M9	246.478	1038.33	2.07474
EAMY_3224,EAMY_3225,EAMY_3226	NC_013961.1:3319572-3323251	M9	M9	172.282	738.548	2.09992
EAMY_3589	NC_013961.1:3678658-3678754	M9	M9	2230.33	9728.03	2.12489
sipB1,spaT1	NC_013961.1:875563-878127	M9	M9	148.71	655.196	2.13943
EAMY_2969	NC_013961.1:3066841-3068581	M9	M9	119.806	531.254	2.14871
hrpA1	NC_013961.1:618237-618465	M9	M9	10959.1	49210.6	2.16684
cysZ	NC_013961.1:2551239-2552001	M9	M9	131.358	599.234	2.18961
EAMY_1929	NC_013961.1:1992842-1992941	M9	M9	7305.46	33816	2.21066
EAMY_1519	NC_013961.1:1584892-1586641	M9	M9	94.0338	437.023	2.21646
sapA,sapB,sapC,sapD,sapF	NC_013961.1:1944415-1949675	M9	M9	369.196	1734.9	2.23239
yfhD	NC_013961.1:2701736-2703659	M9	M9	96.4648	454.039	2.23474
uvrB	NC_013961.1:1284774-1286799	M9	M9	119.539	564.117	2.23852
goaG	NC_013961.1:2463931-2465282	M9	M9	39.5884	187.318	2.24234
ygdR3	NC_013961.1:1629373-1629607	M9	M9	533.097	2569.37	2.26895
yibK	NC_013961.1:126798-127269	M9	M9	131.495	636.378	2.27487
hmsT	NC_013961.1:3140492-3141590	M9	M9	66.3316	332.216	2.32436
prgH1	NC_013961.1:860962-862228	M9	M9	199.207	1001.2	2.32939
yohN	NC_013961.1:887418-887859	M9	M9	852.34	4303.13	2.33589
yejH	NC_013961.1:2371886-2373641	M9	M9	42.0478	217.901	2.37357
EAMY_1776	NC_013961.1:1837274-1837415	M9	M9	1577.28	8305.53	2.39663
yqjA,yqjB	NC_013961.1:3191041-3192105	M9	M9	192.461	1014.85	2.39863
EAMY_0485	NC_013961.1:564579-565848	M9	M9	155.042	821.603	2.40578
EAMY_2449,EAMY_2450,rcsC3	NC_013961.1:2520167-2522316	M9	M9	131.645	719.516	2.45037
EAMY_3260	NC_013961.1:3358947-3360018	M9	M9	173.201	955.226	2.46339
nrdH	NC_013961.1:2786708-2786951	M9	M9	249.013	1392.46	2.48335
EAMY_2076	NC_013961.1:2122832-2123636	M9	M9	63.2541	353.712	2.48335
EAMY_3186	NC_013961.1:3275079-3275175	M9	M9	7137.05	39909.9	2.48335
EAMY_3423	NC_013961.1:3517737-3518052	M9	M9	27.6187	160.619	2.53993
iolD	NC_013961.1:3600351-3602292	M9	M9	13.3859	79.0116	2.56135
alsD	NC_013961.1:29381-30164	M9	M9	72.198	429.813	2.57368
fadA	NC_013961.1:257411-258575	M9	M9	92.0117	554.332	2.59086

artP	NC_013961.1:1383797-1384526	M9	M9	47.7431	288.881	2.59711
lipB	NC_013961.1:1177647-1178373	M9	M9	64.0207	392.422	2.6158
EAMY_2269	NC_013961.1:2319381-2319792	M9	M9	181.194	1133.44	2.6451
ung	NC_013961.1:2723340-2724021	M9	M9	234.276	1466.66	2.64625
EAMY_0859	NC_013961.1:948260-948380	M9	M9	332.601	2107.87	2.66392
EAMY_0795,EAMY_0796	NC_013961.1:881050-883395	M9	M9	533.6	3401.55	2.67236
HopPtoC	NC_013961.1:834954-835868	M9	M9	125.263	827.496	2.72379
mrdA	NC_013961.1:1182367-1184272	M9	M9	69.8617	471.342	2.7542
dfoJ	NC_013961.1:3336922-3338476	M9	M9	80.8039	555.053	2.78013
yghA	NC_013961.1:552539-553433	M9	M9	65.311	454.953	2.80032
EAMY_2592	NC_013961.1:2679289-2679982	M9	M9	128.735	910.865	2.82283
cutC	NC_013961.1:2123869-2124806	M9	M9	139.352	988.792	2.82693
EAMY_1076	NC_013961.1:1145392-1145536	M9	M9	490.67	3566.92	2.86186
nlp3	NC_013961.1:475544-475874	M9	M9	64.1018	485.289	2.92041
panF,yhdT	NC_013961.1:326819-328506	M9	M9	224.948	1745.81	2.95624
ygfP	NC_013961.1:1809790-1811107	M9	M9	93.8955	733.134	2.96495
flhD3	NC_013961.1:2738944-2739295	M9	M9	47.005	372.767	2.98739
EAMY_2384	NC_013961.1:2457112-2457217	M9	M9	9976.73	80185	3.00669
EAMY_3207	NC_013961.1:3296569-3296995	M9	M9	45.8779	368.785	3.00691
EAMY_3021	NC_013961.1:3126061-3126598	M9	M9	15.3776	126.836	3.04406
EAMY_2213	NC_013961.1:2250080-2250185	M9	M9	676.388	5673.47	3.06831
EAMY_0490	NC_013961.1:568840-569023	M9	M9	111.327	964.928	3.11561
EAMY_2759	NC_013961.1:2846946-2847057	M9	M9	7102.27	62750.2	3.14327
EAMY_3204	NC_013961.1:3294265-3295156	M9	M9	33.7344	298.68	3.14631
EAMY_3029	NC_013961.1:3135836-3135944	M9	M9	1083.83	9870.28	3.18695
yfaE	NC_013961.1:2416040-2416301	M9	M9	110.028	1004.94	3.19116
orfB1,ybjR1	NC_013961.1:1385357-1386523	M9	M9	318.348	2931.97	3.20319
ybaV	NC_013961.1:1070002-1070335	M9	M9	67.5626	626.077	3.21204
EAMY_0745	NC_013961.1:834954-835868	M9	M9	464.499	4329.07	3.22031
EAMY_1513	NC_013961.1:1580881-1580974	M9	M9	491.4	4671.38	3.24888
EAMY_3056	NC_013961.1:3156020-3156146	M9	M9	2179.73	21198	3.28171
yebY	NC_013961.1:2095555-2095891	M9	M9	429.965	4338.36	3.33486

elaA	NC_013961.1:2425853-2426315	M9	M9	64.2989	655.495	3.34972
tas	NC_013961.1:777188-778229	M9	M9	133.959	1397.44	3.38292
yqeI	NC_013961.1:3740420-3740864	M9	M9	103.571	1081.1	3.38381
EAMY_3639	NC_013961.1:3733428-3733575	M9	M9	4814.4	52112.9	3.43621
EAMY_1094,EAMY_1095	NC_013961.1:1165419-1165658	M9	M9	107.252	1214.69	3.50152
EAMY_0044	NC_013961.1:66733-69927	M9	M9	151.009	1711.63	3.50266
EAMY_0562	NC_013961.1:639002-639449	M9	M9	36.7274	419.555	3.51393
pyrF,yciH	NC_013961.1:1962959-1964250	M9	M9	323.227	3777.62	3.54686
fliQ3,fliR3	NC_013961.1:2765423-2766472	M9	M9	125.963	1491.5	3.56569
mgsA	NC_013961.1:1473876-1474335	M9	M9	240.164	2943.36	3.61537
ydhB	NC_013961.1:1753778-1755733	M9	M9	118.369	1455.22	3.61987
EAMY_3644	NC_013961.1:3739097-3739721	M9	M9	35.1333	473.219	3.7516
oppA5,oppB3,oppC3,oppD3	NC_013961.1:2211543-2216184	M9	M9	264.037	3669.68	3.79684
EAMY_3093	NC_013961.1:3183394-3184036	M9	M9	38.0975	637.477	4.0646
fldX	NC_013961.1:2015210-2016098	M9	M9	50.8223	855.742	4.07364
EAMY_2553	NC_013961.1:2643151-2644120	M9	M9	63.1489	1105.51	4.12981
EAMY_1879	NC_013961.1:1944097-1944238	M9	M9	94242.5	1.69874e+06	4.17194
ygdL	NC_013961.1:805427-806674	M9	M9	51.7179	944.729	4.19116
EAMY_2539	NC_013961.1:2623117-2624091	M9	M9	360.619	7099.71	4.29921
kdpE	NC_013961.1:1220075-1220756	M9	M9	59.2422	1290.48	4.44514
EAMY_3614	NC_013961.1:3712847-3712955	M9	M9	154.833	3463.26	4.48335
EAMY_0604	NC_013961.1:679754-679865	M9	M9	142.045	3336.09	4.55373
EAMY_2017	NC_013961.1:2076379-2076514	M9	M9	757.601	18640.4	4.62085
EAMY_3568	NC_013961.1:3657952-3658045	M9	M9	245.7	6320.11	4.68498
EAMY_0766	NC_013961.1:853285-853384	M9	M9	202.929	5446.88	4.74638
rpmE2,rpmJ2	NC_013961.1:1082899-1083315	M9	M9	1399.92	42272	4.91628
intS1	NC_013961.1:2651027-2651180	M9	M9	502.37	16068.7	4.99936
EAMY_0296	NC_013961.1:351728-351836	M9	M9	928.998	31515.6	5.08425
intR	NC_013961.1:1902342-1903047	M9	M9	47.4485	1667.98	5.1356
EAMY_1595	NC_013961.1:1657354-1657594	M9	M9	94.008	3916.36	5.38059
EAMY_3336	NC_013961.1:3446241-3446373	M9	M9	774.165	32379.5	5.3863
EAMY_1490	NC_013961.1:1558063-1558162	M9	M9	811.717	36312.5	5.48335

EAMY_0058	NC_013961.1:82748-82874	M9	M9	379.083	18654.3	5.62085
EAMY_2810	NC_013961.1:2899693-2899858	M9	M9	39.1503	2057.9	5.71601
EAMY_3720	NC_013957.1:7163-7322	M9	M9	530.957	31026.8	5.86878
relB	NC_013961.1:2866659-2866887	M9	M9	13.7505	830.429	5.9163
EAMY_1642	NC_013961.1:1708724-1708975	M9	M9	38.2334	3329.25	6.44422
EAMY_2041	NC_013961.1:2096589-2097064	M9	M9	64.9974	10845.5	7.3825
EAMY_1758	NC_013961.1:1819899-1820010	M9	M9	426.136	714717	10.7118
EAMY_0112	NC_013961.1:134419-135520	M9	M9	0	1995.49	1.79769e+308
EAMY_0670	NC_013961.1:743737-743860	M9	M9	0	1947.3	1.79769e+308
EAMY_0580	NC_013961.1:659434-659527	M9	M9	0	21158.6	1.79769e+308
EAMY_2605	NC_013961.1:2692598-2692775	M9	M9	58260.2	104.196	-9.12706
EAMY_2636	NC_013961.1:2722897-2722990	M9	M9	91400.5	274.787	-8.37774
EAMY_0945,EAMY_0946	NC_013961.1:1026107-1026358	M9	M9	121859	546.966	-7.79955
EAMY_0794	NC_013961.1:879481-880828	M9	M9	17153.1	116.974	-7.19614
EAMY_2047	NC_013961.1:2097381-2100526	M9	M9	43299.6	448.908	-6.59179
EAMY_1627	NC_013961.1:1694480-1694582	M9	M9	141931	2276.49	-5.96223
EAMY_3163	NC_013961.1:3249834-3253766	M9	M9	6566.91	114.547	-5.8412
EAMY_1743	NC_013961.1:1806290-1807757	M9	M9	2719.37	48.574	-5.80694
gtrB3	NC_013961.1:3421007-3421931	M9	M9	3565.73	65.014	-5.7773
cybB	NC_013961.1:3639919-3640444	M9	M9	7620.16	176.108	-5.43529
amiA	NC_013961.1:2565573-2566452	M9	M9	2186.68	51.1934	-5.41664
EAMY_0998	NC_013961.1:1079646-1079784	M9	M9	13397.6	315.445	-5.40844
yebU	NC_013961.1:2087571-2088960	M9	M9	2065.27	62.7224	-5.04121
iolC	NC_013961.1:3602785-3604708	M9	M9	1414.57	43.2801	-5.03052
fliZ	NC_013961.1:2180947-2181451	M9	M9	3950.98	121.55	-5.02258
EAMY_1860	NC_013961.1:1927950-1928049	M9	M9	12987.5	453.906	-4.83858
EAMY_3289	NC_013961.1:3395544-3395643	M9	M9	12175.8	453.906	-4.74547
yneJ	NC_013961.1:2341971-2342850	M9	M9	793.424	30.9294	-4.68104
bglA	NC_013961.1:572851-574285	M9	M9	3114.76	122.043	-4.67366
EAMY_1239	NC_013961.1:1312243-1313395	M9	M9	3818.69	161.247	-4.56573
EAMY_3459,glpE	NC_013961.1:3553887-3554348	M9	M9	33378.6	1424.95	-4.54994
proP3	NC_013961.1:3782008-3782437	M9	M9	359.384	15.824	-4.50534

lysR3	NC_013961.1:3649180-3650814	M9	M9	1954.87	89.3471	-4.45151
EAMY_1672	NC_013961.1:1735934-1739102	M9	M9	5352.79	249.437	-4.42355
EAMY_2337	NC_013961.1:2398488-2398620	M9	M9	3912.55	182.322	-4.42355
rfbX,yibD	NC_013961.1:2155189-2157474	M9	M9	1452.03	67.8039	-4.42056
ycfX	NC_013961.1:1592457-1592787	M9	M9	12820.4	606.612	-4.40152
lgt,thyA	NC_013961.1:783933-785603	M9	M9	4575.96	217.656	-4.39395
glpF	NC_013961.1:147430-148264	M9	M9	1259.33	61.6822	-4.35165
fliE1	NC_013961.1:1580150-1580462	M9	M9	899.567	44.292	-4.34411
ampG	NC_013961.1:1055817-1057305	M9	M9	2161.83	107.369	-4.33161
EAMY_0150	NC_013961.1:174577-174670	M9	M9	27518.4	1373.94	-4.32401
EAMY_3230	NC_013961.1:3325817-3326078	M9	M9	8142.08	413.908	-4.29801
gltI	NC_013961.1:1193335-1194338	M9	M9	1200.09	61.5035	-4.28633
EAMY_1620	NC_013961.1:1685851-1687024	M9	M9	1096.59	57.3017	-4.2583
yoaE	NC_013961.1:2073255-2074809	M9	M9	2737.77	144.913	-4.23975
EAMY_2561	NC_013961.1:2647578-2647803	M9	M9	5048.66	268.874	-4.2309
EAMY_0503	NC_013961.1:582023-582218	M9	M9	1899.8	101.177	-4.2309
EAMY_1266	NC_013961.1:1337322-1337463	M9	M9	23067.7	1249.5	-4.20645
EAMY_0699	NC_013961.1:780455-780563	M9	M9	15947.8	865.814	-4.20316
EAMY_3111	NC_013961.1:3196886-3197126	M9	M9	3090.51	170.848	-4.17706
lrgA,ywgG	NC_013961.1:3387341-3388461	M9	M9	3178.73	179.271	-4.14824
EAMY_2584	NC_013961.1:2671924-2672083	M9	M9	3185.74	197.938	-4.00851
ybcQ1	NC_013961.1:1584065-1584434	M9	M9	792.379	51.373	-3.94711
yhhN	NC_013961.1:3592898-3593525	M9	M9	2740.85	188.296	-3.86355
elaC	NC_013961.1:3634681-3635803	M9	M9	817.757	58.743	-3.79918
EAMY_1775	NC_013961.1:1836977-1837148	M9	M9	1078.64	77.8278	-3.79278
yebH	NC_013961.1:2075096-2075993	M9	M9	4019.38	294.883	-3.76876
baeR	NC_013961.1:2317329-2318037	M9	M9	1105.26	82.6925	-3.74049
ygaD	NC_013961.1:889399-889894	M9	M9	1102.46	83.5081	-3.72266
yveA	NC_013961.1:2681003-2682620	M9	M9	1013.79	79.7088	-3.66887
EAMY_3550	NC_013961.1:3642701-3643616	M9	M9	2616.28	212.69	-3.62069
EAMY_1044	NC_013961.1:1120329-1120737	M9	M9	380.066	31.3569	-3.5994
proQ	NC_013961.1:2082034-2082727	M9	M9	4190.46	348.185	-3.58918

proS	NC_013961.1:2818816-2820535	M9	M9	1730.73	143.944	-3.5878
ydiJ	NC_013961.1:1735934-1739102	M9	M9	807.594	70.1636	-3.52484
EAMY_0394	NC_013961.1:463697-463895	M9	M9	1033.14	96.2871	-3.42355
EAMY_2044,exoX	NC_013961.1:2097381-2100526	M9	M9	4880.85	505.975	-3.27
ybjO	NC_013961.1:1380194-1380750	M9	M9	474.805	49.4025	-3.26468
EAMY_2015	NC_013961.1:2075096-2075993	M9	M9	24051.7	2645.27	-3.18465
ydgR	NC_013961.1:1772293-1773772	M9	M9	623.605	69.6298	-3.16286
EAMY_1438	NC_013961.1:1514447-1514612	M9	M9	783.006	87.5702	-3.16051
yhgH	NC_013961.1:3545921-3546635	M9	M9	578.306	64.8178	-3.15737
mmsA	NC_013961.1:3606712-3608218	M9	M9	3712.34	417.456	-3.15263
ltaA	NC_013961.1:1387226-1388231	M9	M9	910.489	102.547	-3.15035
ydaA	NC_013961.1:1885813-1886764	M9	M9	2613.25	301.808	-3.11414
eamA	NC_013961.1:2161754-2162630	M9	M9	713.612	82.4874	-3.11289
cheB3,cheR3	NC_013961.1:2776550-2778454	M9	M9	1178.99	137.944	-3.09539
yehT,yehU	NC_013961.1:585707-588106	M9	M9	1678.93	197.298	-3.08909
pmbA	NC_013961.1:3211892-3213233	M9	M9	1016.23	120.57	-3.07528
EAMY_2963	NC_013961.1:3060926-3061160	M9	M9	1281.97	156.15	-3.03736
lysR1	NC_013961.1:735452-737533	M9	M9	468.788	59.2583	-2.98385
pldB1	NC_013961.1:236598-237222	M9	M9	4353.48	555.221	-2.97103
spaK	NC_013961.1:868542-868950	M9	M9	109.035	13.9364	-2.96787
ychJ	NC_013961.1:2027048-2027510	M9	M9	840.831	107.866	-2.96257
EAMY_3235	NC_013961.1:3334238-3335858	M9	M9	225.672	29.0628	-2.95698
rtn3	NC_013961.1:3610272-3611823	M9	M9	1422.72	183.285	-2.95649
yhcF	NC_013961.1:1928227-1928923	M9	M9	1078.49	140.184	-2.94362
yrbF	NC_013961.1:381725-382538	M9	M9	2550.04	333.158	-2.93624
EAMY_1598,EAMY_1599,rtn2	NC_013961.1:1663923-1666222	M9	M9	15676.1	2056.03	-2.93064
fdhD	NC_013961.1:3747651-3749450	M9	M9	518.388	71.6579	-2.85483
msuD	NC_013961.1:1865609-1866782	M9	M9	189.64	26.7904	-2.82348
EAMY_2455,EAMY_2456	NC_013961.1:2524321-2524646	M9	M9	1975.49	281.928	-2.80881
EAMY_1658,nlpC	NC_013961.1:1722795-1723397	M9	M9	3888.38	560.611	-2.7941
EAMY_2166	NC_013961.1:2208095-2208284	M9	M9	575.952	84.0178	-2.77718
hrpK	NC_013961.1:594695-596984	M9	M9	577.308	84.5621	-2.77126

EAMY_2140	NC_013961.1:2182370-2183339	M9	M9	385.629	56.4998	-2.7709
zntA	NC_013961.1:3593617-3595876	M9	M9	185.494	27.4261	-2.75775
yhhF,yhhL	NC_013961.1:3591917-3592785	M9	M9	3378.41	499.793	-2.75694
ydcR	NC_013961.1:559391-560861	M9	M9	945.606	142.527	-2.73
yleB	NC_013961.1:1200732-1201911	M9	M9	1124.91	173.07	-2.70039
yifB	NC_013961.1:185281-186802	M9	M9	927.714	143.052	-2.69714
EAMY_1697	NC_013961.1:1763497-1763725	M9	M9	797.527	123.026	-2.69656
gltP	NC_013961.1:3380701-3382003	M9	M9	3697.09	572.285	-2.69159
EAMY_1756	NC_013961.1:1818332-1818443	M9	M9	5113.63	794.307	-2.68658
EAMY_0390,EAMY_0391,EAMY_0392	NC_013961.1:458089-462796	M9	M9	2003.23	314.115	-2.67296
flgB1	NC_013961.1:1524417-1524831	M9	M9	345.202	54.1851	-2.67147
EAMY_1750	NC_013961.1:1813552-1814710	M9	M9	329.127	52.1525	-2.65784
araG	NC_013961.1:1790183-1791695	M9	M9	138.656	22.0742	-2.65108
EAMY_2274	NC_013961.1:2324005-2324215	M9	M9	24706	3944.41	-2.64698
EAMY_1554	NC_013961.1:1616854-1617058	M9	M9	410.47	65.5806	-2.64594
rhtB3	NC_013961.1:3355633-3356260	M9	M9	1066.31	171.333	-2.63775
trkA	NC_013961.1:3467267-3468644	M9	M9	636.956	105.809	-2.58974
EAMY_0055	NC_013961.1:80154-81519	M9	M9	590.17	99.4406	-2.56922
apaG,ksgA,pdxA,surA	NC_013961.1:3020581-3024053	M9	M9	3916.29	661.99	-2.56461
yfhC	NC_013961.1:2701736-2703659	M9	M9	1237.93	209.614	-2.56213
EAMY_3094,EAMY_3095	NC_013961.1:3184040-3185182	M9	M9	7924.6	1355.51	-2.5475
vanA	NC_013961.1:3641545-3642580	M9	M9	141.9	24.2818	-2.54693
pbpG	NC_013961.1:1301375-1302326	M9	M9	444.02	76.1751	-2.54323
dgt	NC_013961.1:2855049-2856555	M9	M9	1127.24	193.482	-2.54252
ampC	NC_013961.1:592010-593243	M9	M9	476.953	82.7112	-2.52769
araC	NC_013961.1:1792704-1793601	M9	M9	112.409	19.7405	-2.50952
recG,spoU	NC_013961.1:70165-72942	M9	M9	676.004	122.041	-2.46967
flgH1	NC_013961.1:1528825-1529527	M9	M9	474.742	86.567	-2.45525
EAMY_1768	NC_013961.1:1831922-1832132	M9	M9	872.813	159.37	-2.45329
EAMY_3267	NC_013961.1:3367027-3367765	M9	M9	138.425	25.5776	-2.43615
prc	NC_013961.1:2079999-2082015	M9	M9	1137.5	211.297	-2.42853
inlA	NC_013961.1:1145893-1147363	M9	M9	931.842	175.023	-2.41254

EAMY_2030	NC_013961.1:2089642-2090452	M9	M9	614.639	117.535	-2.38665
ybeB	NC_013961.1:1184780-1185098	M9	M9	534.136	102.579	-2.38048
fliF1,fliG1,fliH1,fliI1	NC_013961.1:1575156-1579910	M9	M9	5354.01	1029.18	-2.37912
yidR	NC_013961.1:3764987-3766599	M9	M9	175.893	33.8343	-2.37814
EAMY_1921	NC_013961.1:1988195-1988321	M9	M9	644441	124962	-2.36655
gcvH	NC_013961.1:715676-716063	M9	M9	865.87	170.434	-2.34494
yejL	NC_013961.1:2375360-2375588	M9	M9	2777.59	553.619	-2.32687
ppx	NC_013961.1:2635066-2636593	M9	M9	1209.4	241.707	-2.32296
citA	NC_013961.1:550838-552161	M9	M9	1219.31	244.362	-2.31897
ygbF,ygbT	NC_013961.1:2903661-2904865	M9	M9	875.99	176.842	-2.30846
EAMY_0231	NC_013961.1:274520-274682	M9	M9	2994.98	604.778	-2.30807
EAMY_1269	NC_013961.1:1338742-1342208	M9	M9	718.838	145.726	-2.30241
EAMY_0373	NC_013961.1:432619-433465	M9	M9	205.486	42.5993	-2.27014
yqhC	NC_013961.1:543247-544165	M9	M9	521.249	109.935	-2.24532
htrA	NC_013961.1:2853444-2854902	M9	M9	1406.47	300.436	-2.22695
EAMY_2953	NC_013961.1:3053740-3053890	M9	M9	6166.99	1319.44	-2.22464
argD	NC_013961.1:3512870-3514088	M9	M9	793.07	170.706	-2.21594
otsA1,otsB	NC_013961.1:2146335-2148550	M9	M9	2603.21	560.375	-2.21583
motA1,motB1	NC_013961.1:2142382-2144295	M9	M9	1608.62	347.878	-2.20917
EAMY_1647	NC_013961.1:1713000-1713162	M9	M9	1289.5	279.128	-2.20782
yeeS	NC_013961.1:466216-466687	M9	M9	109.978	24.0647	-2.19222
EAMY_3538	NC_013961.1:3629956-3630439	M9	M9	755.483	166.424	-2.18254
fliO1,fliP1	NC_013961.1:1570257-1571381	M9	M9	646.328	143.105	-2.1752
EAMY_3088	NC_013961.1:3177980-3178130	M9	M9	1608.78	359.847	-2.16051
fpr	NC_013961.1:140891-142072	M9	M9	335.037	75.4697	-2.15035
ptrB	NC_013961.1:2097381-2100526	M9	M9	379.606	85.7795	-2.1458
fliD3	NC_013961.1:2755026-2756496	M9	M9	728.957	165.331	-2.14047
yqfA	NC_013961.1:720726-721386	M9	M9	870.093	198.399	-2.13277
spaS3	NC_013961.1:1649344-1650436	M9	M9	69.6813	16.2355	-2.10162
amsK,amsL	NC_013961.1:2280396-2282957	M9	M9	1909.77	449.047	-2.08846
yhcA	NC_013961.1:1929012-1929717	M9	M9	121.827	28.6842	-2.08651
EAMY_2968	NC_013961.1:3065747-3066749	M9	M9	758.889	180.581	-2.07124

yeiE	NC_013961.1:2350734-2351619	M9	M9	307.215	74.0029	-2.0536
acs	NC_013961.1:3382509-3384465	M9	M9	418.791	101.425	-2.04582
inh	NC_013961.1:3672278-3672683	M9	M9	787.034	190.888	-2.0437
EAMY_3696	NC_013961.1:3789784-3790102	M9	M9	248.184	60.3404	-2.04022
amtB	NC_013961.1:1077342-1078644	M9	M9	428.87	104.47	-2.03745
yhjJ1,yhjK1,yhjL	NC_013961.1:700091-703157	M9	M9	2283.11	556.727	-2.03596
pagO	NC_013961.1:1071640-1072651	M9	M9	190.011	46.4298	-2.03296
fadB	NC_013961.1:258585-260772	M9	M9	358.369	88.5392	-2.01706
invA3,invB	NC_013961.1:1641644-1644111	M9	M9	387.805	96.0109	-2.01406
yigQ	NC_013961.1:120942-121869	M9	M9	553.982	137.46	-2.01083
EAMY_3654	NC_013961.1:3747651-3749450	M9	M9	1074.07	266.581	-2.01044
flgC1	NC_013961.1:1524834-1525239	M9	M9	1080.99	268.658	-2.00851
yadB	NC_013961.1:2880054-2880963	M9	M9	249.322	62.3045	-2.0006
engA	NC_013961.1:2661711-2663211	M9	M9	516.918	129.212	-2.00019
yfhH	NC_013961.1:2705775-2706615	M9	M9	134.566	33.9465	-1.98697
EAMY_3729	NC_013957.1:15254-15647	M9	M9	1278.82	322.831	-1.98597
fliS1	NC_013961.1:2185951-2186350	M9	M9	862.777	218.472	-1.98154
yicE	NC_013961.1:66733-69927	M9	M9	478.602	121.791	-1.97442
fliT1	NC_013961.1:2186362-2186728	M9	M9	786.973	200.428	-1.97323
EAMY_1815	NC_013961.1:1883499-1883664	M9	M9	2740.52	700.562	-1.96787
flgG1	NC_013961.1:1527953-1528736	M9	M9	295.457	75.7763	-1.96313
emrR	NC_013961.1:2796153-2796684	M9	M9	927.655	238.576	-1.95914
EAMY_1539	NC_013961.1:1606631-1606808	M9	M9	1614.89	416.784	-1.95406
sdhA,sdhC,sdhD	NC_013961.1:1230425-1232922	M9	M9	6156.54	1602.39	-1.9419
waaG,waaQ3	NC_013961.1:109968-112166	M9	M9	367.009	95.6893	-1.93939
yciU	NC_013961.1:1994720-1995044	M9	M9	1082.29	282.431	-1.93812
speC	NC_013961.1:656194-658339	M9	M9	211.678	55.462	-1.9323
EAMY_3341	NC_013961.1:3452394-3452547	M9	M9	5777.25	1516.98	-1.92919
polB	NC_013961.1:3010813-3013177	M9	M9	134.912	35.7972	-1.9141
rpmJ	NC_013961.1:3475795-3475912	M9	M9	33176.9	8872.83	-1.90271
cheY1	NC_013961.1:2133175-2133565	M9	M9	828.429	224.953	-1.88075
EAMY_1270	NC_013961.1:1338742-1342208	M9	M9	198.176	53.9723	-1.87649

flhA3,flhB3,flhE3	NC_013961.1:2779544-2783214	M9	M9	265.357	72.6701	-1.8685
EAMY_0242	NC_013961.1:290947-291502	M9	M9	215.311	59.1797	-1.86325
yhhK	NC_013961.1:3586968-3587376	M9	M9	380.066	104.523	-1.86243
yraL	NC_013961.1:3197902-3199381	M9	M9	967.385	266.161	-1.86179
hha	NC_013961.1:1081000-1081219	M9	M9	3040.8	837.117	-1.86095
EAMY_1759	NC_013961.1:1820273-1821026	M9	M9	85.4849	23.5738	-1.85848
fliL1	NC_013961.1:1572795-1573278	M9	M9	185.437	51.2073	-1.85651
recQ	NC_013961.1:234706-236539	M9	M9	218.035	60.2966	-1.85441
flgA1	NC_013961.1:1523594-1524263	M9	M9	530.26	148.259	-1.83858
ydbL	NC_013961.1:1915939-1916272	M9	M9	714.233	199.697	-1.83858
tap3	NC_013961.1:2135616-2137224	M9	M9	294.265	82.2753	-1.83858
EAMY_2707	NC_013961.1:2785256-2785739	M9	M9	602.097	168.984	-1.83311
prgJ3,prgK3	NC_013961.1:1634860-1635963	M9	M9	354.304	101.242	-1.80718
yeeO	NC_013961.1:2248491-2249961	M9	M9	155.477	44.4685	-1.80585
ychF	NC_013961.1:1662478-1663570	M9	M9	594.468	171.285	-1.7952
EAMY_0370	NC_013961.1:430147-430243	M9	M9	36354.4	10476.3	-1.79499
sufE	NC_013961.1:1745321-1745744	M9	M9	438.798	126.749	-1.79159
yvrE	NC_013961.1:2525239-2526124	M9	M9	379.056	109.947	-1.7856
EAMY_1063	NC_013961.1:1135316-1135622	M9	M9	683.464	199.402	-1.77718
sulA	NC_013961.1:1467348-1467855	M9	M9	329.193	96.7612	-1.76643
trpI	NC_013961.1:1096318-1097194	M9	M9	137.933	40.7081	-1.76058
gntK,gntU	NC_013961.1:3569083-3571039	M9	M9	521.685	155.707	-1.74435
crcA	NC_013961.1:1173901-1174528	M9	M9	215.385	64.4618	-1.7404
EAMY_3288	NC_013961.1:3395294-3395450	M9	M9	4570.53	1370.12	-1.73806
EAMY_1249,EAMY_1250	NC_013961.1:1319700-1320678	M9	M9	193.822	58.2544	-1.73429
ycgZ	NC_013961.1:1630746-1630992	M9	M9	970.995	292.839	-1.72935
EAMY_2461	NC_013961.1:2526614-2526896	M9	M9	1364.72	412.507	-1.72611
flhC1,flhD1	NC_013961.1:2144320-2145361	M9	M9	3296.7	1006.43	-1.71177
EAMY_3554,EAMY_3555	NC_013961.1:3645877-3646851	M9	M9	555.38	172.15	-1.68981
cheB1,cheR1	NC_013961.1:2133667-2135589	M9	M9	414.37	128.59	-1.68814
EAMY_3575	NC_013961.1:3666250-3667162	M9	M9	402.872	125.101	-1.68723
rpmB	NC_013961.1:103618-103855	M9	M9	2063.22	655.377	-1.6545

sbcC,sbcD	NC_013961.1:1013619-1018202	M9	M9	278.683	90.1187	-1.62873
yifA	NC_013961.1:183963-184791	M9	M9	488.748	159.139	-1.6188
yejB,yejE	NC_013961.1:2365332-2367449	M9	M9	908.878	299.582	-1.60114
holB,pabC,tmk,yceG	NC_013961.1:1546872-1550332	M9	M9	1103.05	365.368	-1.59408
yfhB	NC_013961.1:2703823-2704462	M9	M9	292.111	97.3479	-1.5853
ggt3	NC_013961.1:943742-945329	M9	M9	119.022	40.1946	-1.56615
proV,proW	NC_013961.1:2790889-2793246	M9	M9	301.353	108.247	-1.47712
EAMY_3008,EAMY_3009	NC_013961.1:3116677-3118062	M9	M9	463.793	168.508	-1.46066
EAMY_3006,EAMY_3007	NC_013961.1:3113723-3116659	M9	M9	265.373	98.1019	-1.43567
EAMY_3017,EAMY_3018	NC_013961.1:3122786-3123720	M9	M9	1732.85	688.329	-1.33198
flgI1,flgJ1	NC_013961.1:1529536-1531584	M9	M9	560.098	224.075	-1.3217
emrB1,hlyD	NC_013961.1:1349296-1352004	M9	M9	189.12	75.7195	-1.32057
rplP,rpmC,rpsQ	NC_013961.1:3481488-3482344	M9	M9	36278.4	15273.3	-1.2481
mdtA,mdtB,mdtC	NC_013961.1:764094-771676	M9	M9	408.677	174.56	-1.22724
cheA3,cheW3,motA3,motB3	NC_013961.1:2734023-2738285	M9	M9	321.088	138.655	-1.21147
hisA,hisF,hisI	NC_013961.1:2261911-2264012	M9	M9	748.812	331.064	-1.17749
dppD3,dppF	NC_013961.1:3706901-3708879	M9	M9	427.364	192.01	-1.15428
ygcB,ygcJ,ygcK,ygcL	NC_013961.1:2906162-2911861	M9	M9	512.618	284.306	-0.850438

Table 2 All significantly differentially expressed transcripts from *in planta* experiments comparing ΔT6SS-C1C3 to the *E. amylovora* wild type strain

E. amylovora locus tag or name	locus	ΔT6SS-C1C3	WT	FPKM_1	FPKM_2	log2(fold_change)
ampC	NC_013961.1:592010-593243	Flower	Flower	2132.44	67.6281	-4.97874
cheA1	NC_013961.1:2140383-2142372	Flower	Flower	929.006	1458.11	0.650337
cheB1,cheR1	NC_013961.1:2133667-2135589	Flower	Flower	1129.48	1747.88	0.629952
cheY1	NC_013961.1:2133175-2133565	Flower	Flower	2133.81	3922.69	0.87841
cheZ1	NC_013961.1:2132517-2133162	Flower	Flower	1222.08	1933.15	0.661611
cstA	NC_013961.1:588546-590700	Flower	Flower	336.249	204.872	-0.71481
cysC,cysN	NC_013961.1:843940-845978	Flower	Flower	491.962	923.962	0.909288
cysI3,cysJ	NC_013961.1:836681-840199	Flower	Flower	450.46	661.475	0.554289
dgkA	NC_013961.1:3437045-3437411	Flower	Flower	144.304	0	-1.79769e+308
EAMY_0661	NC_013961.1:734346-734970	Flower	Flower	580.365	921.265	0.666656

EAMY_0934,EAMY_0935	NC_013961.1:1012569-1013570	Flower	Flower	497.598	1011.75	1.02379
EAMY_1906	NC_013961.1:1970685-1970901	Flower	Flower	4759.55	8573.45	0.849051
EAMY_2140	NC_013961.1:2182370-2183339	Flower	Flower	507.087	885.744	0.804656
EAMY_2477	NC_013961.1:2545330-2546586	Flower	Flower	817.012	1947.51	1.2532
EAMY_3020	NC_013961.1:3124558-3126058	Flower	Flower	4.53674	478.651	6.72118
EAMY_3021	NC_013961.1:3126061-3126598	Flower	Flower	0	635.192	1.79769e+308
EAMY_3046,EAMY_3047	NC_013961.1:3149716-3150543	Flower	Flower	416.018	39.7798	-3.38654
EAMY_3521	NC_013961.1:3615013-3615736	Flower	Flower	40.7849	0	-1.79769e+308
EAMY_3529,EAMY_3530	NC_013961.1:3620426-3621754	Flower	Flower	32.7553	1005.44	4.93995
EAMY_3565	NC_013961.1:3654216-3655761	Flower	Flower	103.037	180.526	0.809035
EAMY_3573,kdpA	NC_013961.1:3663424-3665184	Flower	Flower	2714.44	10.2098	-8.05455
EAMY_3721	NC_013957.1:7440-8997	Flower	Flower	781.14	1527.57	0.967589
fabB	NC_013961.1:2495483-2496707	Flower	Flower	377.513	631.818	0.742982
flgL1	NC_013961.1:1533393-1534359	Flower	Flower	1457.83	2512.86	0.785515
fliC1	NC_013961.1:2183410-2184253	Flower	Flower	14815.7	34163.8	1.20534
metE	NC_013961.1:242742-245016	Flower	Flower	78.1252	141.825	0.860249
motA1,motB1	NC_013961.1:2142382-2144295	Flower	Flower	2476.83	3546.8	0.518025
phoH	NC_013961.1:2167738-2168527	Flower	Flower	178.292	341.192	0.936343
pspA	NC_013961.1:1942245-1942917	Flower	Flower	602.511	1046.55	0.796583
pstA3,pstC3	NC_013961.1:3784292-3786139	Flower	Flower	81.6798	194.245	1.24983
pstS3	NC_013961.1:3786233-3787265	Flower	Flower	86.9628	200.947	1.20835
rcsV	NC_013961.1:2890263-2890941	Flower	Flower	353.219	89.2995	-1.98384
sdhA,sdhC,sdhD	NC_013961.1:1230425-1232922	Flower	Flower	1451.98	732.286	-0.98754
tauA	NC_013961.1:3505210-3506188	Flower	Flower	112.01	218.863	0.966407
tauB,tauC,tauD3	NC_013961.1:3502767-3505195	Flower	Flower	203.704	439.046	1.10789
tsr3	NC_013961.1:2138022-2139687	Flower	Flower	516.155	809.881	0.649905
tsr7	NC_013961.1:3216653-3218219	Flower	Flower	825.626	1375.29	0.736175
yddG	NC_013961.1:583485-584382	Flower	Flower	38.1629	0	-1.79769e+308
yfiA	NC_013961.1:913474-913813	Flower	Flower	1150.27	2102.42	0.870084
yhhW	NC_013961.1:3572407-3573103	Flower	Flower	585.1	1026.29	0.81069
ykfE	NC_013961.1:593247-593694	Flower	Flower	1496.95	223.671	-2.74258
ymcA,ymcB	NC_013961.1:3442198-3445008	Flower	Flower	354.186	538.452	0.604308

Table 3 All significantly differentially expressed *M. x domestica* transcripts in response to *E. amylovora* two days post inoculation

M. x domestica accession no.	*M. x domestica* loci	log2(fold_change)	*A. thaliana* accession no.	Name	Description
MDP0000756448	MDC000011.378: 16806-16970	1.79769e+308	AT5G46630.2		Clathrin adaptor complexes medium subunit family protein
MDP0000268505	MDC000020.209: 8435-13377	-4.53718	AT1G29980.1		Protein of unknown function, DUF642
0	MDC000127.652: 4251-4492	1.79769e+308	AT4G33720.1		CAP (Cysteine-rich secretory proteins, Antigen 5, and Pathogenesis-related 1 protein) superfamily protein
MDP0000163276	MDC000130.277: 7155-7601	2.19171	AT5G43380.1	TOPP6	type one serine/threonine protein phosphatase 6
MDP0000659818	MDC000144.408: 251-3627	1.79769e+308	AT2G39200.1	ATMLO12, MLO12	Seven transmembrane MLO family protein
MDP0000417927	MDC000149.326: 14929-15724	-1.93472	AT2G34430.1	LHB1B1, LHCB1.4	light-harvesting chlorophyll-protein complex II subunit B1
MDP0000417929	MDC000149.326: 17749-18547	-1.87154	AT2G34430.1	LHB1B1, LHCB1.4	light-harvesting chlorophyll-protein complex II subunit B1
MDP0000601491	MDC000149.357: 271-1069	-1.87058	AT2G34430.1	LHB1B1, LHCB1.4	light-harvesting chlorophyll-protein complex II subunit B1
MDP0000235175	MDC000149.357: 3094-3889	-1.80257	AT2G34430.1	LHB1B1, LHCB1.4	light-harvesting chlorophyll-protein complex II subunit B1
MDP0000265831	MDC000164.370: 18851-32386	2.71647	AT5G41770.1		crooked neck protein, putative / cell cycle protein, putative
MDP0000161380	MDC000178.398: 6450-13590	1.79769e+308	AT5G19485.1		transferases;nucleotidyltransferases
MDP0000256732	MDC000211.300: 6961-7241	1.79769e+308	AT2G18290.1	APC10	anaphase promoting complex 10
MDP0000255157	MDC000270.326: 10081-10388	1.79769e+308	AT4G21430.1	B160	Zinc finger, RING-type;Transcription factor jumonji/aspartyl beta-hydroxylase
0	MDC000319.348: 8176-8367	-2.48801			
MDP0000265100	MDC000357.185: 21423-36365	2.72442	AT5G23760.1		Copper transport protein family
MDP0000264101	MDC000368.238: 2725-8711	1.79769e+308	AT4G05410.1	YAO	Transducin/WD40 repeat-like superfamily protein
0	MDC000416.247: 30134-30295	1.79769e+308			
0	MDC000446.497: 2613-3451	2.36105	AT3G19615.1		unknown protein
0	MDC000455.144: 3026-3468	3.21257	AT4G24620.1	PGI1, PGI	phosphoglucose isomerase 1
MDP0000323652	MDC000503.259: 1794-2875	2.4077			
MDP0000263664	MDC000567.258: 7588-8550	-2.52714	AT4G25040.1		Uncharacterised protein family (UPF0497)
MDP0000639167	MDC000600.439: 7351-10850	1.79769e+308	AT2G45220.1		Plant invertase/pectin methylesterase inhibitor superfamily
MDP0000134666	MDC000618.395: 5589-5886	1.79769e+308	AT1G62930.1		Tetratricopeptide repeat (TPR)-like superfamily protein
MDP0000146621	MDC000636.590: 1152-4139	1.79769e+308	AT5G20080.1		FAD/NAD(P)-binding oxidoreductase
MDP0000413403	MDC000636.613: 20700-20894	1.79769e+308	AT1G80160.1		Lactoylglutathione lyase / glyoxalase I family protein
MDP0000256199	MDC000662.220: 27328-27666	1.79769e+308	AT3G63440.1	ATCKX6, ATCKX7, CKX6	cytokinin oxidase/dehydrogenase 6
MDP0000268130	MDC000695.201: 7077-7269	1.79769e+308	AT1G09660.1		RNA-binding KH domain-containing protein
MDP0000262910	MDC000703.490: 1546-15062	1.79769e+308	AT3G23940.1		dehydratase family
MDP0000235454	MDC000704.27: 983-1106	1.79769e+308	AT5G47720.2		Thiolase family protein
0	MDC000706.497: 11518-11660	1.79769e+308			
MDP0000903417	MDC000706.499: 3489-5017	1.79769e+308	AT1G61560.1	ATMLO6, MLO6	Seven transmembrane MLO family protein
MDP0000119183	MDC000707.178: 9077-13361	7.01306	AT5G13830.1		FtsJ-like methyltransferase family protein
MDP0000757070	MDC000711.381: 8991-9419	-2.27797	AT5G38760.1		Late embryogenesis abundant protein (LEA) family protein
MDP0000119262	MDC000769.371: 651-2301	1.70216	AT3G26430.1		GDSL-like Lipase/Acylhydrolase superfamily protein

MDP0000256865	MDC000791.288: 5104-7135	1.79769e+308	AT4G10490.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000265644	MDC000810.342: 26666-27910	1.79769e+308	AT1G52800.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000264592	MDC000841.228: 2232-8160	4.28011	AT5G20230.1	ATBCB, BCB, SAG14	blue-copper-binding protein
MDP0000268271	MDC000866.255: 10198-10455	1.79769e+308	AT1G31930.1	XLG3	extra-large GTP-binding protein 3
MDP0000264034	MDC000886.330: 32493-36293	1.79769e+308	AT4G03180.1		
MDP0000503940	MDC000913.258: 27076-29046	2.37597	AT3G11180.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000361449	MDC000929.194: 1888-3055	-3.06288	AT3G16520.3	UGT88A1	UDP-glucosyl transferase 88A1
MDP0000052862	MDC000929.235: 4940-6389	-3.0507	AT3G16520.3	UGT88A1	UDP-glucosyl transferase 88A1
MDP0000846313	MDC001071.282: 19208-19513	1.79769e+308	AT3G10760.1		Homeodomain-like superfamily protein
MDP0000134250	MDC001204.784: 1228-4995	-1.79053	AT1G53280.1		Class I glutamine amidotransferase-like superfamily protein
MDP0000803538	MDC001240.396: 9691-9990	1.79769e+308	AT3G03940.1		Protein kinase family protein
MDP0000159558	MDC001261.116: 13665-20797	1.79769e+308	AT4G32160.1		Phox (PX) domain-containing protein
MDP0000265913	MDC001262.249: 1127-4650	1.95271	AT5G47770.1	FPS1	farnesyl diphosphate synthase 1
MDP0000445218	MDC001273.205: 845-1730	1.79769e+308	AT1G02680.1	TAF13	TBP-associated factor 13
MDP0000235782	MDC001276.321: 32854-33398	1.79769e+308	AT4G18160.1	ATKCO6, ATTPK3, KCO6, TPK3	Ca2+ activated outward rectifying K+ channel 6
MDP0000119600	MDC001284.344: 1341-1621	1.79769e+308	AT2G45760.1	BAL, BAP2	BON association protein 2
0	MDC001441.272: 13692-14163	1.79769e+308	AT5G43920.1		transducin family protein / WD-40 repeat family protein
0	MDC001471.424: 93507-93619	1.79769e+308	AT2G29260.1		NAD(P)-binding Rossmann-fold superfamily protein
MDP0000527355	MDC001500.115: 2484-4397	-1.88554	AT1G05850.1	ATCTL1, CTL1, ELP, ELP1, ERH2, HOT2, POM1	Chitinase family protein
MDP0000706016	MDC001647.167: 31621-31880	1.79769e+308	AT1G32360.1		Zinc finger (CCCH-type) family protein
MDP0000498524	MDC001659.508: 3688-13621	1.79769e+308	AT1G22380.1	AtUGT85A3, UGT85A3	UDP-glucosyl transferase 85A3
0	MDC001671.165: 2805-2973	1.79769e+308	AT1G78380.1	ATGSTU19, GST8, GSTU19	glutathione S-transferase TAU 19
MDP0000496027	MDC001715.358: 1470-1791	1.79769e+308	AT4G36220.1	CYP84A1, FAH1	ferulic acid 5-hydroxylase 1
MDP0000268417	MDC001733.221: 3341-3606	1.79769e+308	AT3G59200.1		F-box/RNI-like superfamily protein
MDP0000163727	MDC001753.378: 36916-37587	1.79769e+308	AT2G15780.1		Cupredoxin superfamily protein
MDP0000159000	MDC001757.664: 1294-3548	3.69176	AT3G11180.2		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000576922	MDC001757.678: 208-6183	4.517	AT2G36690.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000340981	MDC001781.94: 3875-6197	1.79769e+308	AT1G28120.1		
MDP0000877084	MDC001787.334: 3408-3753	1.79769e+308			
MDP0000265806	MDC001831.292: 8893-9169	2.3957			
MDP0000588582	MDC001839.110: 1393-3069	-2.34333	AT1G68220.1		Protein of unknown function (DUF1218)
MDP0000264961	MDC001845.296: 622-3441	1.79769e+308	AT5G20885.1		RING/U-box superfamily protein
MDP0000533638	MDC001848.381: 1843-2323	3.75248	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000831518	MDC001848.391: 1325-1805	5.13328	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000831519	MDC001848.391: 5087-5567	4.99847	AT1G24020.1	MLP423	MLP-like protein 423
0	MDC001867.380: 3629-3727	1.79769e+308			
0	MDC001900.112: 16993-17583	-2.04989			
0	MDC001938.226: 2272-2436	1.79769e+308			

MDP0000607969	MDC001963.417: 459-4217	2.78368	AT4G27250.1		NAD(P)-binding Rossmann-fold superfamily protein
0	MDC001963.417: 4816-4925	1.79769e+308	AT4G27250.2		NAD(P)-binding Rossmann-fold superfamily protein
MDP0000025413	MDC001972.273: 3026-9072	2.43751	AT5G27450.1	MK, MVK	mevalonate kinase
MDP0000844719	MDC001977.912: 3360-3668	1.79769e+308			
MDP0000267282	MDC001999.548: 8598-8811	1.79769e+308	AT1G80400.1		RING/U-box superfamily protein
MDP0000452572	MDC002001.729: 20293-31469	1.71884	AT3G53990.1		Adenine nucleotide alpha hydrolases-like superfamily protein
0	MDC002052.246: 9559-9831	1.79769e+308			
MDP0000829170	MDC002080.143: 3807-5483	1.79769e+308	AT5G19440.1		NAD(P)-binding Rossmann-fold superfamily protein
MDP0000873573	MDC002124.224: 10772-12083	3.23587	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein
MDP0000515106	MDC002124.224: 5558-6883	2.49012	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein
MDP0000707567	MDC002124.226: 5571-6882	2.42596	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein
MDP0000120175	MDC002136.624: 799-1408	1.79769e+308	AT1G68760.1	ATNUDT1, ATNUDX1, NUDX1	nudix hydrolase 1
0	MDC002136.660: 2651-2671	4.09695			
0	MDC002149.751: 1345-1407	1.79769e+308			
0	MDC002149.751: 2007-2430	2.48927			
0	MDC002218.355: 6778-7176	1.79769e+308			
0	MDC002270.126: 3680-3863	1.79769e+308			
MDP0000163984	MDC002285.447: 6979-7069	1.79769e+308	AT4G18530.1		Protein of unknown function (DUF707)
MDP0000157186	MDC002285.478: 30943-31155	1.79769e+308	AT4G16444.1		
MDP0000266136	MDC002304.132: 819-8300	-2.53248	AT1G14220.1		Ribonuclease T2 family protein
MDP0000457389	MDC002306.103: 1840-2063	1.79769e+308	AT5G58350.1	WNK4, ZIK2	with no lysine (K) kinase 4
0	MDC002322.251: 26803-27928	4.61002	AT4G11280.1	ACS6, ATACS6	1-aminocyclopropane-1-carboxylic acid (acc) synthase 6
MDP0000837051	MDC002335.203: 3094-5164	1.79769e+308	AT1G50430.1	7RED, DWF5, LE, PA, ST7R	Ergosterol biosynthesis ERG4/ERG24 family
0	MDC002385.280: 8975-9237	1.79769e+308			
MDP0000165382	MDC002388.638: 6966-12223	1.79769e+308	AT2G41770.1		Protein of unknown function (DUF288)
MDP0000268597	MDC002412.301: 3820-15392	1.79769e+308	AT5G27640.1	ATEIF3B-1, ATTIF3B1, EIF3B, EIF3B-1, TIF3B1	translation initiation factor 3B1
MDP0000164286	MDC002413.411: 10891-11713	-2.76725	AT5G14920.1		Gibberellin-regulated family protein
MDP0000269551	MDC002413.411: 4634-4664	1.79769e+308	AT5G14920.1		Gibberellin-regulated family protein
0	MDC002431.300: 11772-11965	1.79769e+308	AT5G19130.2		GPI transamidase component family protein / Gaa1-like family protein
MDP0000236390	MDC002446.247: 7797-8476	1.79769e+308	AT3G05950.1		RmlC-like cupins superfamily protein
MDP0000833077	MDC002505.371: 15860-16380	1.79769e+308	AT1G63700.1	EMB71, MAPKKK4, YDA	Protein kinase superfamily protein
MDP0000897416	MDC002555.575: 20823-21885	1.80749			
MDP0000062070	MDC002587.522: 8090-8266	1.79769e+308	AT5G04620.2	ATBIOF, BIOF	biotin F
MDP0000525437	MDC002618.102: 55-788	1.79769e+308	AT1G20760.1		Calcium-binding EF hand family protein
MDP0000265800	MDC002672.379: 8552-21592	1.79769e+308	AT2G22300.1	CAMTA3, SR1	signal responsive 1
MDP0000840722	MDC002693.97: 512-884	1.79769e+308	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000236536	MDC002765.351: 2478-6149	2.51354	AT3G25150.2		Nuclear transport factor 2 (NTF2) family protein with RNA binding (RRM-RBD-RNP motifs) domain
MDP0000155698	MDC002771.180: 9590-12097	-2.80764	AT4G25150.1		HAD superfamily, subfamily IIIB acid phosphatase

MDP0000699497	MDC002791.491: 4020-6869	-1.84137			
0	MDC002799.293: 2023-2423	2.25333	AT2G29330.1	TRI	tropinone reductase
MDP0000361511	MDC002827.323: 10419-11049	-3.81975	AT3G22142.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000788170	MDC002892.343: 26056-27195	3.94434	AT1G78780.2		pathogenesis-related family protein
MDP0000236618	MDC002931.100: 11631-11924	1.79769e+308	AT3G12345.1		
MDP0000173465	MDC002957.519: 16454-16916	2.88122	AT4G38240.1	CGL, CGL1, GNTI	alpha-1, 3-mannosyl-glycoprotein beta-1, 2-N-acetylglucosaminyltransferase, putative
MDP0000885511	MDC002975.216: 22992-23382	2.46881	AT3G56710.1	SIB1	sigma factor binding protein 1
MDP0000167437	MDC003038.458: 3206-3383	1.79769e+308	AT2G33580.1		Protein kinase superfamily protein
MDP0000120758	MDC003093.180: 517-1215	2.722	AT4G25370.1		Double Clp-N motif protein
MDP0000146334	MDC003164.614: 3761-6028	-2.65594	AT2G45960.2	ATHH2, PIP1;2, PIP1B, TMP-A	plasma membrane intrinsic protein 1B
MDP0000274905	MDC003165.207: 2450-6779	1.79769e+308	AT4G20000.1		VQ motif-containing protein
MDP0000120819	MDC003190.148: 129-814	1.79769e+308	AT2G36690.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
0	MDC003190.186: 1345-1510	1.79769e+308			
0	MDC003236.290: 5639-6048	-2.12497			
MDP0000637694	MDC003261.485: 10664-15893	1.8661	AT1G48320.1		Thioesterase superfamily protein
0	MDC003306.225: 3010-3406	-1.81213	AT2G16850.1	PIP3B, PIP2;8	plasma membrane intrinsic protein 2;8
MDP0000155343	MDC003320.570: 27284-27737	-2.50676	AT4G14890.1		2Fe-2S ferredoxin-like superfamily protein
MDP0000233708	MDC003334.452: 3099-5117	3.43165			
MDP0000276241	MDC003359.104: 24766-32452	1.79769e+308	AT3G43860.1	AtGH9A4, GH9A4	glycosyl hydrolase 9A4
MDP0000270966	MDC003384.296: 5308-10574	1.79769e+308	AT5G44280.1	ATRING1A, RING1A	RING 1A
MDP0000146255	MDC003415.452: 19197-19538	2.55638	AT3G14470.1		NB-ARC domain-containing disease resistance protein
MDP0000272795	MDC003436.247: 8739-9967	3.41978	AT5G66170.3	STR18	sulfurtransferase 18
MDP0000134791	MDC003451.570: 18763-21683	-2.29196	AT5G05270.1		Chalcone-flavanone isomerase family protein
0	MDC003469.231: 3820-4226	1.79769e+308			
MDP0000427722	MDC003504.134: 67401-67998	-2.42477	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000593502	MDC003507.409: 7615-7888	1.79769e+308	AT1G07880.2	ATMPK13	Protein kinase superfamily protein
0	MDC003508.304: 714-802	1.79769e+308			
MDP0000271527	MDC003560.581: 10762-10811	1.79769e+308	AT3G26040.1		HXXXD-type acyl-transferase family protein
0	MDC003571.122: 29326-29962	3.67188			
MDP0000121058	MDC003620.800: 295-3822	1.79769e+308	AT3G60640.1	ATG8G	Ubiquitin-like superfamily protein
MDP0000277042	MDC003638.527: 2878-5280	1.79769e+308			
MDP0000170501	MDC003661.185: 59137-59369	1.79769e+308	AT1G03370.1		C2 calcium/lipid-binding and GRAM domain containing protein
MDP0000680997	MDC003670.313: 733-3535	1.79769e+308	AT1G77120.1	ADH, ADH1, ATADH, ATADH1	alcohol dehydrogenase 1
MDP0000147293	MDC003688.191: 1671-3161	2.53723	AT4G34100.1		RING/U-box superfamily protein
0	MDC003716.306: 46958-47066	1.79769e+308	AT1G03260.1		SNARE associated Golgi protein family
0	MDC003741.386: 2317-2600	1.79769e+308			
MDP0000391319	MDC003758.191: 289-1601	3.01485	AT5G04550.1		Protein of unknown function (DUF668)

0	MDC003761.240: 3013-3454	2.52991			
MDP0000276506	MDC003761.240: 7197-17791	4.45347			
MDP0000441166	MDC003788.290: 5474-5635	1.79769e+308	AT2G38800.1		Plant calmodulin-binding protein-related
MDP0000276278	MDC003807.231: 14012-14233	1.79769e+308	AT4G28500.1	ANAC073, NAC073, SND2	NAC domain containing protein 73
MDP0000787808	MDC003810.272: 15817-16803	1.79769e+308	AT4G12350.1	AtMYB42, MYB42	myb domain protein 42
MDP0000273012	MDC003865.562: 8097-8515	1.79769e+308	AT3G54040.1		PAR1 protein
MDP0000167303	MDC003919.355: 3369-5166	-1.74607	AT1G01780.1		GATA type zinc finger transcription factor family protein
MDP0000171644	MDC003966.297: 5407-5482	1.79769e+308	AT5G66900.1		Disease resistance protein (CC-NBS-LRR class) family
MDP0000237113	MDC004009.559: 4179-15094	1.79769e+308	AT3G18290.1	BTS, EMB2454	zinc finger protein-related
MDP0000854767	MDC004013.428: 929-2727	1.79769e+308	AT3G12270.1	ATPRMT3, PRMT3	protein arginine methyltransferase 3
0	MDC004047.206: 4467-4494	1.79769e+308			
MDP0000830926	MDC004049.516: 1567-2569	2.10525	AT5G16080.1	AtCXE17, CXE17	carboxyesterase 17
0	MDC004050.111: 2972-3698	2.97995			
0	MDC004050.111: 8000-8340	1.79769e+308			
MDP0000169311	MDC004086.357: 2616-11039	1.79769e+308	AT3G45140.1	ATLOX2, LOX2	lipoxygenase 2
MDP0000135837	MDC004095.241: 944-5617	1.60314	AT1G60140.1	ATTPS10, TPS10	trehalose phosphate synthase
0	MDC004097.232: 8798-9675	3.40094	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
0	MDC004133.336: 8038-8299	1.79769e+308			
MDP0000564592	MDC004154.351: 39-6072	1.79769e+308	AT5G13180.1	ANAC083, NAC083, VNI2	NAC domain containing protein 83
MDP0000487384	MDC004165.256: 2099-4204	-1.8127	AT5G23860.1	TUB8	tubulin beta 8
MDP0000155233	MDC004175.403: 24292-27127	-2.1379	AT1G75060.1		
MDP0000951190	MDC004175.403: 6190-7715	1.79769e+308	AT5G42610.1		Protein of unknown function (DUF607)
MDP0000147913	MDC004193.226: 2939-4271	1.79769e+308	AT4G10490.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000168767	MDC004225.334: 10573-10850	1.79769e+308			
MDP0000174018	MDC004233.457: 20199-20679	2.2613	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000864747	MDC004233.457: 6800-7280	5.22546	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000864748	MDC004233.457: 9098-9578	4.01462	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000175004	MDC004259.286: 9836-10513	1.79769e+308			
MDP0000167080	MDC004293.550: 16904-17262	1.79769e+308	AT1G14610.1	TWN2, VALRS	valyl-tRNA synthetase / valine--tRNA ligase (VALRS)
MDP0000167088	MDC004293.550: 69667-71109	1.79769e+308	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein
MDP0000913358	MDC004324.263: 15880-16063	1.79769e+308	AT5G67630.1		P-loop containing nucleoside triphosphate hydrolases superfamily protein
MDP0000170316	MDC004331.378: 24044-24882	-2.69079	AT1G32560.1		Late embryogenesis abundant protein, group 1 protein
MDP0000147581	MDC004374.399: 19-1173	1.79769e+308	AT5G61820.1		
MDP0000167786	MDC004427.577: 2224-5046	-1.95698	AT1G73760.1		RING/U-box superfamily protein
0	MDC004475.200: 15597-16341	5.32451	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000137468	MDC004475.200: 20541-21775	3.67923	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000121566	MDC004513.349: 138-370	1.79769e+308	AT2G14520.1		CBS domain-containing protein with a domain of unknown function (DUF21)
MDP0000065495	MDC004571.195: 2433-4815	1.79769e+308	AT5G47080.1	CKB1	casein kinase II beta chain 1
MDP0000166057	MDC004613.228: 11547-12800	1.79769e+308	AT5G05200.1		Protein kinase superfamily protein

MDP0000170777	MDC004652.210: 48970-50473	1.79769e+308	AT5G53045.1		
MDP0000166875	MDC004673.395: 10875-13759	-1.9178	AT2G38170.3	ATCAX1, CAX1, RCI4	cation exchanger 1
MDP0000249060	MDC004678.229: 17526-20215	1.79769e+308	AT3G20640.1		basic helix-loop-helix (bHLH) DNA-binding superfamily protein
MDP0000421679	MDC004696.296: 3968-4432	1.79769e+308	AT5G47910.1	ATRBOHD, RBOHD	respiratory burst oxidase homologue D
MDP0000237403	MDC004719.334: 21812-23054	2.25432	AT5G42570.1		B-cell receptor-associated 31-like
MDP0000557465	MDC004732.225: 9663-9840	1.79769e+308	AT2G19730.1		Ribosomal L28e protein family
MDP0000553127	MDC004757.363: 10617-19812	2.12939	AT3G51680.1		NAD(P)-binding Rossmann-fold superfamily protein
MDP0000168735	MDC004766.533: 4405-5962	1.79769e+308	AT5G13930.1	ATCHS, CHS, TT4	Chalcone and stilbene synthase family protein
MDP0000716308	MDC004766.552: 11190-11877	1.79769e+308	AT5G13930.1	ATCHS, CHS, TT4	Chalcone and stilbene synthase family protein
MDP0000913661	MDC004804.396: 7723-8379	1.88284	AT3G04300.1		RmlC-like cupins superfamily protein
0	MDC004821.392: 9339-9512	1.79769e+308			
0	MDC004849.513: 20-284	1.79769e+308			
MDP0000271982	MDC004885.793: 4041-27077	5.6005	AT2G39340.1		SAC3/GANP/Nin1/mts3/eIF-3 p25 family
0	MDC004932.328: 15182-15442	1.79769e+308			
MDP0000136847	MDC004932.329: 23136-23429	1.79769e+308	AT1G73050.1		Glucose-methanol-choline (GMC) oxidoreductase family protein
0	MDC004932.329: 29625-30381	3.26688			
MDP0000566117	MDC004936.114: 731-11600	2.28845	AT4G20030.1		RNA-binding (RRM/RBD/RNP motifs) family protein
MDP0000170531	MDC004966.470: 3884-8290	3.33886	AT1G70520.1	CRK2	cysteine-rich RLK (RECEPTOR-like protein kinase) 2
MDP0000148873	MDC004989.363: 3672-5602	1.4007	AT4G27450.1		Aluminium induced protein with YGL and LRDR motifs
MDP0000121897	MDC005009.620: 1896-3950	1.90789	AT1G27450.1	APT1, ATAPT1	adenine phosphoribosyl transferase 1
MDP0000147784	MDC005054.249: 5101-5480	1.79769e+308	AT3G59110.1		Protein kinase superfamily protein
MDP0000137705	MDC005122.196: 4548-6205	2.24	AT1G78440.1	ATGA2OX1, GA2OX1	Arabidopsis thaliana gibberellin 2-oxidase 1
MDP0000166259	MDC005161.483: 10-1556	2.00714	AT2G38740.1		Haloacid dehalogenase-like hydrolase (HAD) superfamily protein
MDP0000275092	MDC005161.724: 3466-11719	1.85637	AT2G38740.1		Haloacid dehalogenase-like hydrolase (HAD) superfamily protein
0	MDC005194.219: 3090-3360	1.79769e+308			
MDP0000658768	MDC005200.174: 34013-34414	3.23991	AT1G11090.1		alpha/beta-Hydrolases superfamily protein
MDP0000702868	MDC005243.382: 9372-10625	2.27364	AT3G54420.1	ATCHITIV, ATEP3, CHIV, EP3	homolog of carrot EP3-3 chitinase
0	MDC005257.231: 6449-6485	1.79769e+308			
0	MDC005259.535: 4241-4601	1.79769e+308			
MDP0000273224	MDC005334.309: 206-8584	-2.16795	AT5G53350.1	CLPX	CLP protease regulatory subunit X
MDP0000450601	MDC005362.240: 6098-12887	1.79769e+308	AT3G11820.2	AT-SYR1, ATSYP121, ATSYR1, PEN1, SYP121, SYR1	syntaxin of plants 121
MDP0000169025	MDC005381.283: 29450-29871	1.79769e+308	AT1G12775.1		Pentatricopeptide repeat (PPR) superfamily protein
MDP0000678615	MDC005398.50: 11698-13402	1.79769e+308	AT1G18400.1	BEE1	BR enhanced expression 1
MDP0000275383	MDC005401.171: 13854-19232	1.79769e+308	AT5G01410.1	ATPDX1, ATPDX1.3, PDX1, PDX1.3, RSR4	Aldolase-type TIM barrel family protein
MDP0000680695	MDC005410.203: 4497-7949	1.79769e+308	AT5G18310.1		
MDP0000167207	MDC005423.311: 6010-6700	3.44525	AT3G23240.1	ATERF1, ERF1	ethylene response factor 1
MDP0000249227	MDC005445.136: 25859-31825	2.11406	AT3G53620.1	AtPPa4, PPa4	pyrophosphorylase 4

0	MDC005456.101: 31462-31741	-2.20103			
0	MDC005479.52: 19099-19266	1.79769e+308			
0	MDC005490.240: 8153-8416	1.79769e+308	AT5G66180.3		S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
MDP0000273966	MDC005490.243: 32160-37061	2.95771	AT5G66160.1	ATRMR1, RMR1	receptor homology region transmembrane domain ring H2 motif protein 1
MDP0000273394	MDC005605.679: 12982-15465	4.02694	AT1G06650.2		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
0	MDC005625.410: 4432-4879	1.79769e+308			
MDP0000257243	MDC005640.206: 3033-6196	4.45015	AT1G73050.1		Glucose-methanol-choline (GMC) oxidoreductase family protein
0	MDC005648.396: 5701-5725	1.79769e+308			
MDP0000679280	MDC005665.223: 5730-9206	1.87481	AT3G16770.1	ATEBP, EBP, ERF72, RAP2.3	ethylene-responsive element binding protein
MDP0000807958	MDC005672.143: 42154-43198	-3.70623	AT5G51550.1	EXL3	EXORDIUM like 3
MDP0000271007	MDC005673.323: 4405-10172	1.73266	AT3G53970.1		proteasome inhibitor-related
MDP0000275079	MDC005673.340: 1858-2675	2.64139	AT3G53970.1		proteasome inhibitor-related
MDP0000276802	MDC005701.391: 5438-9015	-2.13886	AT1G64090.1	RTNLB3	Reticulan like protein B3
0	MDC005717.700: 845-1059	1.79769e+308			
MDP0000271088	MDC005717.708: 36286-47025	1.79769e+308	AT1G79830.1	GC5	golgin candidate 5
MDP0000784851	MDC005723.274: 5102-5374	1.79769e+308	AT1G49000.1		
MDP0000931239	MDC005735.253: 3467-3929	-1.71542	AT4G05320.2	UBQ10	polyubiquitin 10
MDP0000624279	MDC005778.440: 252-801	1.79769e+308	AT4G20000.1		VQ motif-containing protein
MDP0000178868	MDC005799.514: 759-806	-2.33718	AT5G17680.1		disease resistance protein (TIR-NBS-LRR class), putative
MDP0000232692	MDC005811.341: 23198-25119	2.96568	AT5G53560.1	ATB5-A, ATCB5-E, B5 #2, CB5-E	cytochrome B5 isoform E
0	MDC005828.284: 3570-4032	1.79769e+308			
MDP0000257423	MDC005856.445: 16813-19559	1.45823	AT2G37430.1		C2H2 and C2HC zinc fingers superfamily protein
MDP0000776042	MDC005857.333: 10992-11123	1.79769e+308	AT3G07700.3		Protein kinase superfamily protein
0	MDC005890.119: 17882-18863	2.27453			
MDP0000279409	MDC005893.621: 7340-26688	1.79769e+308	AT1G50030.1	TOR	target of rapamycin
0	MDC005927.393: 5902-6584	3.89137	AT5G10830.1		S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
MDP0000280686	MDC005983.384: 14695-15478	1.79769e+308	AT4G13180.1		NAD(P)-binding Rossmann-fold superfamily protein
MDP0000507805	MDC005987.255: 1295-1536	1.82319	AT2G38470.1	ATWRKY33, WRKY33	WRKY DNA-binding protein 33
MDP0000282531	MDC005992.425: 10230-24855	1.79769e+308	AT2G16230.1		O-Glycosyl hydrolases family 17 protein
MDP0000713750	MDC006022.710: 6794-7361	1.79769e+308	AT4G37710.1		VQ motif-containing protein
MDP0000281307	MDC006067.226: 2770-5589	1.79769e+308	AT5G07910.1		Leucine-rich repeat (LRR) family protein
MDP0000280867	MDC006113.282: 7307-21521	1.79769e+308	AT5G25757.1		RNA polymerase I-associated factor PAF67
MDP0000233439	MDC006132.110: 38822-42176	1.79769e+308	AT2G31955.1	CNX2	cofactor of nitrate reductase and xanthine dehydrogenase 2
MDP0000233439	MDC006132.110: 42437-42590	1.79769e+308	AT2G31955.1	CNX2	cofactor of nitrate reductase and xanthine dehydrogenase 2
MDP0000233440	MDC006132.110: 44034-44983	2.81494	AT2G31945.1		
MDP0000344124	MDC006216.151: 1502-1745	1.79769e+308			
MDP0000280820	MDC006246.458: 682-958	2.04655			
0	MDC006260.462: 8079-8672	2.73287	AT1G23440.1		Peptidase C15, pyroglutamyl peptidase I-like
MDP0000281098	MDC006273.129: 20610-22757	-2.5382	AT5G51440.1		HSP20-like chaperones superfamily protein

MDP0000238184	MDC006273.74: 424-2967	-2.52469	AT5G51440.1		HSP20-like chaperones superfamily protein
MDP0000032171	MDC006283.261: 35240-41767	-1.94697	AT1G09310.1		Protein of unknown function, DUF538
0	MDC006289.408: 7320-7584	-2.07297	AT2G45960.3	PIP1B, TMP-A, ATHH2, PIP1;2	plasma membrane intrinsic protein 1B
0	MDC006290.363: 14600-14871	1.79769e+308			
MDP0000279018	MDC006290.371: 8651-11538	3.88462	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000327743	MDC006290.371: 8651-11538	4.09612			
MDP0000921896	MDC006365.287: 19008-19524	-2.93166	AT5G09530.1		hydroxyproline-rich glycoprotein family protein
MDP0000278727	MDC006365.296: 8642-9158	-3.15338	AT5G09530.1		hydroxyproline-rich glycoprotein family protein
0	MDC006367.239: 347-584	1.79769e+308			
MDP0000278697	MDC006377.327: 14719-15944	-2.64093			
MDP0000366350	MDC006462.291: 4203-4755	-2.0333			
MDP0000279102	MDC006464.260: 445-1034	2.00176	AT2G42160.1	BRIZ1	zinc finger (ubiquitin-hydrolase) domain-containing protein
MDP0000940872	MDC006465.421: 24406-24762	4.01979	AT1G70160.1		
MDP0000694318	MDC006473.444: 2709-3675	1.79769e+308	AT1G70250.1		receptor serine/threonine kinase, putative
MDP0000657053	MDC006504.484: 24167-26272	-1.92738	AT4G14960.2	TUA6	Tubulin/FtsZ family protein
MDP0000281041	MDC006515.236: 1405-3722	3.37856	AT3G02850.1	SKOR	STELAR K+ outward rectifier
MDP0000410264	MDC006528.136: 5057-7941	-1.9936	AT2G37640.1	ATEXP3, ATEXPA3, ATHEXP ALPHA 1.9, EXP3	Barwin-like endoglucanases superfamily protein
MDP0000773502	MDC006536.318: 82895-83101	1.79769e+308	AT5G64560.1	ATMGT9, MGT9, MRS2-2	magnesium transporter 9
MDP0000234325	MDC006553.299: 18189-18514	3.21243	AT1G32230.2	ATP8, CEO, CEO1, RCD1	WWE protein-protein interaction domain protein family
MDP0000182716	MDC006600.356: 5806-6097	1.93603	AT3G14470.1		NB-ARC domain-containing disease resistance protein
0	MDC006603.734: 2300-2410	4.51059	AT5G39110.1		RmlC-like cupins superfamily protein
MDP0000182713	MDC006603.747: 276-4246	1.80959	AT3G26430.1		GDSL-like Lipase/Acylhydrolase superfamily protein
MDP0000635152	MDC006630.203: 6162-6951	1.79769e+308	AT2G36690.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000843913	MDC006630.345: 13587-14886	1.79304	AT2G36690.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000552328	MDC006653.435: 4109-5236	2.26965	AT1G75800.1		Pathogenesis-related thaumatin superfamily protein
MDP0000249299	MDC006684.239: 7756-10611	-2.91344	AT3G21190.1		O-fucosyltransferase family protein
MDP0000249161	MDC006776.974: 7590-21009	1.79769e+308	AT4G34580.1	COW1, SRH1	Sec14p-like phosphatidylinositol transfer family protein
MDP0000405576	MDC006783.229: 11986-13497	1.79769e+308	AT1G52343.1		
MDP0000614645	MDC006784.251: 4983-11622	2.1349	AT3G25655.1	IDL1	inflorescence deficient in abscission (IDA)-like 1
0	MDC006793.328: 2502-2994	2.61703			
0	MDC006793.328: 4674-5465	2.2282			
MDP0000248822	MDC006817.441: 6965-9324	5.62372	AT2G26560.1	PLA IIA, PLA2A, PLP2	phospholipase A 2A
MDP0000814329	MDC006848.168: 4784-9157	2.62974	AT3G06650.1	ACLB-1	ATP-citrate lyase B-1
MDP0000805422	MDC006858.526: 1099-1672	1.86738	AT4G17500.1	ATERF-1, ERF-1	ethylene responsive element binding factor 1
MDP0000343634	MDC006858.527: 5849-6150	-3.44095			
MDP0000238475	MDC006888.339: 876-1073	1.79769e+308	AT3G30300.1		O-fucosyltransferase family protein
MDP0000178516	MDC006898.720: 8191-8834	-2.21317	AT1G65295.1		
MDP0000136298	MDC006922.133: 31989-32562	-3.54702	AT5G09530.1		hydroxyproline-rich glycoprotein family protein

MDP0000248516	MDC006922.133: 35876-36560	-3.84131	AT5G09530.1		hydroxyproline-rich glycoprotein family protein
MDP0000137117	MDC006985.165: 1223-3076	-1.92555	AT3G11400.1	ATEIF3G1, EIF3G1	eukaryotic translation initiation factor 3G1
0	MDC006994.179: 16210-16462	1.79769e+308			
0	MDC006995.271: 38249-38468	1.79769e+308			
MDP0000184167	MDC006998.275: 5023-5392	1.79769e+308	AT1G80770.2	PDE318	P-loop containing nucleoside triphosphate hydrolases superfamily protein
MDP0000617009	MDC007021.246: 25478-25865	-2.50768	AT2G46600.1		Calcium-binding EF-hand family protein
0	MDC007024.343: 8632-8930	2.35329			
MDP0000182364	MDC007070.485: 4341-4878	-2.28142	AT5G38760.1		Late embryogenesis abundant protein (LEA) family protein
MDP0000805474	MDC007073.330: 12070-12457	1.79769e+308	AT3G09270.1	ATGSTU8, GSTU8	glutathione S-transferase TAU 8
0	MDC007088.513: 4786-5156	1.79769e+308	AT5G24810.2		ABC1 family protein
MDP0000279516	MDC007100.397: 805-12837	1.79769e+308	AT2G18470.1	PERK4	roline-rich extensin-like receptor kinase 4
MDP0000249404	MDC007109.204: 49-2474	1.79769e+308	AT4G00590.1		N-terminal nucleophile aminohydrolases (Ntn hydrolases) superfamily protein
MDP0000147996	MDC007197.415: 11084-11948	1.79769e+308	AT3G08690.1	ATUBC11, UBC11	ubiquitin-conjugating enzyme 11
MDP0000176426	MDC007216.431: 6443-7603	1.79769e+308	AT1G68450.1		VQ motif-containing protein
0	MDC007223.300: 45679-45974	-2.75104			
MDP0000729533	MDC007236.83: 16404-17781	1.79769e+308	AT3G26040.1		HXXXD-type acyl-transferase family protein
MDP0000181621	MDC007245.594: 763-2225	1.79769e+308	AT3G08880.1		
MDP0000693594	MDC007269.339: 4912-5995	2.40891	AT4G37300.1	MEE59	maternal effect embryo arrest 59
MDP0000279107	MDC007287.149: 7106-7274	1.79769e+308	AT2G27980.1		Acyl-CoA N-acyltransferase with RING/FYVE/PHD-type zinc finger domain
MDP0000811844	MDC007352.390: 11700-12258	1.82193			
0	MDC007364.345: 4479-4876	1.8905			
MDP0000147939	MDC007394.331: 695-1727	-2.14127	AT3G55430.1		O-Glycosyl hydrolases family 17 protein
MDP0000180472	MDC007395.672: 2994-3955	-2.52714	AT4G25040.1		Uncharacterised protein family (UPF0497)
MDP0000175691	MDC007406.309: 1539-2750	1.79769e+308	AT1G52800.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000123467	MDC007407.185: 1806-1906	1.79769e+308	AT5G13080.1	ATWRKY75, WRKY75	WRKY DNA-binding protein 75
MDP0000123467	MDC007407.185: 1980-2255	1.79769e+308	AT5G13080.1	ATWRKY75, WRKY75	WRKY DNA-binding protein 75
MDP0000282711	MDC007441.706: 4194-6829	1.9862	AT3G13710.1	PRA1.F4	prenylated RAB acceptor 1.F4
MDP0000231813	MDC007467.200: 80611-80777	1.79769e+308	AT3G62580.1		Late embryogenesis abundant protein (LEA) family protein
0	MDC007474.161: 727-1187	2.13649			
MDP0000281921	MDC007517.244: 8152-8403	1.79769e+308	AT4G02920.1		
MDP0000231711	MDC007566.303: 5209-5295	1.79769e+308	AT3G25590.1		
0	MDC007581.595: 2473-2576	1.79769e+308	AT4G28460.1		unknown protein
MDP0000178934	MDC007586.376: 13849-14356	-1.89038	AT2G25770.1		Polyketide cyclase/dehydrase and lipid transport superfamily protein
MDP0000238852	MDC007632.133: 37-1671	1.79769e+308	AT5G15860.1	ATPCME, PCME	prenylcysteine methylesterase
MDP0000943804	MDC007651.256: 10903-11228	1.79769e+308	AT4G32320.1	APX6	ascorbate peroxidase 6
MDP0000281059	MDC007667.245: 11085-11336	1.79769e+308	AT1G71980.1		Protease-associated (PA) RING/U-box zinc finger family protein
MDP0000462809	MDC007696.347: 224-1274	-2.36735	AT4G32390.1		Nucleotide-sugar transporter family protein
MDP0000284756	MDC007726.450: 6011-6496	-1.90333	AT1G78880.1		Ubiquitin-specific protease family C19-related protein
0	MDC007779.587: 2989-3343	1.79769e+308	AT3G14630.1	CYP72A14	cytochrome P450, family 72, subfamily A, polypeptide 14

0	MDC007779.587: 3489-4308	5.81577	AT3G14680.1	CYP72A9	cytochrome P450, family 72, subfamily A, polypeptide 9
MDP0000320004	MDC007801.297: 1668-14062	-2.60268	AT4G30600.1		signal recognition particle receptor alpha subunit family protein
MDP0000279567	MDC007839.76: 255-4737	-1.98232	AT1G35140.1	EXL7, PHI-1	Phosphate-responsive 1 family protein
MDP0000279568	MDC007839.76: 6045-12451	1.79769e+308	AT5G16800.2		Acyl-CoA N-acyltransferases (NAT) superfamily protein
MDP0000177906	MDC007908.251: 15906-18464	3.66793	AT1G80840.1	ATWRKY40, WRKY40	WRKY DNA-binding protein 40
MDP0000156208	MDC007970.423: 2201-3402	1.79769e+308	AT5G17820.1		Peroxidase superfamily protein
0	MDC008017.329: 6473-7175	2.01024	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000176969	MDC008031.166: 10358-10802	-1.71749	AT2G33820.1	ATMBAC1, MBAC1	Mitochondrial substrate carrier family protein
0	MDC008031.166: 8984-9384	-1.91543	AT3G60030.1	SPL12	squamosa promoter-binding protein-like 12
0	MDC008070.309: 6943-7245	1.79769e+308			
MDP0000178304	MDC008095.233: 439-1308	1.79769e+308	AT3G09270.1	ATGSTU8, GSTU8	glutathione S-transferase TAU 8
MDP0000180902	MDC008107.194: 8214-8566	1.79769e+308	AT1G52800.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000176147	MDC008111.220: 3257-3489	1.79769e+308	AT3G08010.1	ATAB2	RNA binding
0	MDC008132.437: 2842-3005	1.79769e+308			
MDP0000282113	MDC008133.431: 23701-30184	-2.02622	AT5G39710.1	EMB2745	Tetratricopeptide repeat (TPR)-like superfamily protein
MDP0000124013	MDC008156.258: 1804-1941	1.79769e+308	AT4G13250.1	NYC1	NAD(P)-binding Rossmann-fold superfamily protein
0	MDC008185.596: 848-1396	4.18103			
MDP0000124065	MDC008191.272: 1308-2582	1.33928	AT2G27830.1		
0	MDC008212.493: 3616-4058	-2.22497	AT5G43180.1		Protein of unknown function, DUF599
0	MDC008216.318: 26921-27156	1.79769e+308	AT4G20820.1		FAD-binding Berberine family protein
0	MDC008227.470: 6-265	2.67388			
MDP0000248806	MDC008228.299: 15226-24695	1.79769e+308	AT3G26070.1		Plastid-lipid associated protein PAP / fibrillin family protein
MDP0000280265	MDC008231.317: 2716-4497	2.51441	AT5G24090.1	ATCHIA, CHIA	chitinase A
MDP0000182082	MDC008275.176: 13207-16686	1.834	AT1G10670.1	ACLA-1	ATP-citrate lyase A-1
MDP0000149907	MDC008363.128: 1345-1577	3.47723	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein
MDP0000149907	MDC008363.128: 1584-2882	2.61724	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein
MDP0000281408	MDC008378.283: 5092-5500	1.92703	AT1G36370.1	SHM7	serine hydroxymethyltransferase 7
0	MDC008382.148: 13043-13406	1.79769e+308			
MDP0000281701	MDC008389.364: 4307-10927	-2.13921	AT2G34770.1	ATFAH1, FAH1	fatty acid hydroxylase 1
MDP0000279279	MDC008406.198: 19837-20128	1.79769e+308	AT4G21390.1	B120	S-locus lectin protein kinase family protein
MDP0000836165	MDC008510.241: 8559-10423	3.04968	AT4G02330.1	ATPMEPCRB	Plant invertase/pectin methylesterase inhibitor superfamily
0	MDC008521.354: 1264-1327	1.79769e+308			
MDP0000720186	MDC008527.309: 2198-2323	1.79769e+308	AT2G34250.1		SecY protein transport family protein
MDP0000857802	MDC008558.180: 29014-29454	1.79769e+308	AT1G30950.1	UFO	F-box family protein
0	MDC008563.271: 10114-10663	2.28791	AT1G75620.1		glyoxal oxidase-related protein
MDP0000149770	MDC008563.295: 2531-3710	1.79769e+308	AT5G40240.2		nodulin MtN21 /EamA-like transporter family protein
MDP0000873376	MDC008586.420: 17793-18695	-1.96409	AT1G72230.1		Cupredoxin superfamily protein
0	MDC008600.171: 902-1400	4.88147			
MDP0000285032	MDC008614.269: 11939-16468	2.46831	AT3G18830.1	ATPLT5, ATPMT5, PMT5	polyol/monosaccharide transporter 5

MDP0000670527	MDC008741.603: 1444-2027	-2.4068	AT2G27420.1		Cysteine proteinases superfamily protein
MDP0000124372	MDC008769.540: 981-2223	1.79769e+308	AT2G35930.1	PUB23	plant U-box 23
MDP0000190474	MDC008769.546: 2266-3508	1.79769e+308	AT2G35930.1	PUB23	plant U-box 23
MDP0000191423	MDC008781.274: 12188-14442	2.96124	AT1G22170.1		Phosphoglycerate mutase family protein
MDP0000191423	MDC008781.274: 14553-14944	2.64127	AT1G22170.1		Phosphoglycerate mutase family protein
MDP0000288293	MDC008798.391: 19315-20212	5.12026	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000185506	MDC008808.256: 4241-10398	-2.75566	AT5G12190.1		RNA-binding (RRM/RBD/RNP motifs) family protein
MDP0000188275	MDC008847.375: 4627-4939	1.79769e+308	AT1G56660.1		
MDP0000287351	MDC008886.243: 375-5075	1.79769e+308	AT5G36930.2		Disease resistance protein (TIR-NBS-LRR class) family
MDP0000694597	MDC008926.173: 3439-3781	-2.3258	AT5G59320.1	LTP3	lipid transfer protein 3
MDP0000773415	MDC008930.262: 14990-15201	1.79769e+308	AT1G05180.1	AXR1	NAD(P)-binding Rossmann-fold superfamily protein
MDP0000290937	MDC008947.382: 14535-20023	3.12302			
MDP0000347336	MDC008953.300: 591-12745	2.93419			
0	MDC008958.527: 6035-6390	1.79769e+308			
MDP0000188138	MDC008981.224: 3552-6255	1.79769e+308	AT5G21940.1		
MDP0000090732	MDC009045.262: 43011-46844	2.52716	AT5G48100.1	ATLAC15, LAC15, TT10	Laccase/Diphenol oxidase family protein
MDP0000291620	MDC009067.527: 8837-9392	-2.07458	AT1G58170.1		Disease resistance-responsive (dirigent-like protein) family protein
MDP0000287628	MDC009095.320: 4320-11111	-1.76609	AT3G58810.1	ATMTP3, ATMTPA2, MTP3, MTPA2	metal tolerance protein A2
MDP0000193050	MDC009100.720: 14269-19338	2.72097	AT5G26340.1	ATSTP13, MSS1, STP13	Major facilitator superfamily protein
0	MDC009100.743: 10602-10864	1.79769e+308			
0	MDC009139.374: 7848-8934	2.91798	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000746652	MDC009231.274: 4163-4333	1.79769e+308	AT1G58440.1	SQE1, XF1	FAD/NAD(P)-binding oxidoreductase family protein
MDP0000138090	MDC009247.159: 1041-7164	2.43611	AT2G47800.1	ATMRP4, EST3, MRP4	multidrug resistance-associated protein 4
MDP0000841703	MDC009250.269: 24582-24915	1.79769e+308	AT3G11440.1	ATMYB65, MYB65	myb domain protein 65
MDP0000361876	MDC009251.558: 7920-10453	-3.37738	AT4G03210.1	XTH9	xyloglucan endotransglucosylase/hydrolase 9
0	MDC009291.198: 2462-2529	1.79769e+308			
MDP0000124719	MDC009297.162: 8847-9498	-1.9762	AT5G47610.1		RING/U-box superfamily protein
MDP0000239720	MDC009336.266: 5288-15663	2.26922	AT5G05930.1	ATGC1, GC1	guanylyl cyclase 1
MDP0000671324	MDC009349.320: 566-1709	1.79769e+308	AT4G10490.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000504527	MDC009360.278: 896-3116	3.05153	AT1G78860.1		D-mannose binding lectin protein with Apple-like carbohydrate-binding domain
MDP0000262674	MDC009368.194: 14350-15917	-1.88738	AT1G07473.1		
0	MDC009393.166: 1252-1510	1.79769e+308			
MDP0000685425	MDC009404.603: 2897-8558	1.79769e+308	AT5G17680.1		disease resistance protein (TIR-NBS-LRR class), putative
MDP0000941000	MDC009483.39: 12100-14889	2.87019	AT1G47670.1		Transmembrane amino acid transporter family protein
MDP0000290562	MDC009567.313: 17183-20584	-1.89197	AT3G55770.1		GATA type zinc finger transcription factor family protein
MDP0000936748	MDC009600.163: 20757-21849	-1.7773	AT2G33850.1		
MDP0000150032	MDC009604.192: 12640-14455	1.79769e+308	AT4G13220.1		
MDP0000285243	MDC009616.38: 20066-24921	2.38728	AT4G19810.1		Glycosyl hydrolase family protein with chitinase insertion domain
MDP0000285243	MDC009616.38: 20066-24921	1.79769e+308	AT4G19810.1		Glycosyl hydrolase family protein with chitinase insertion domain

0	MDC009630.367: 24050-24262	1.79769e+308	AT2G03810.4		18S pre-ribosomal assembly protein gar2-related
MDP0000187983	MDC009673.411: 12650-17839	1.79769e+308	AT2G41040.1		S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
MDP0000290045	MDC009727.218: 5205-32777	1.79769e+308	AT2G42810.2	PAPP5, PP5, PP5.2	protein phosphatase 5.2
MDP0000125002	MDC009738.162: 4550-8590	1.79769e+308	AT1G26810.1	GALT1	galactosyltransferase1
MDP0000757636	MDC009757.32: 1532-2923	-1.71887	AT3G08940.2	LHCB4.2	light harvesting complex photosystem II
MDP0000193574	MDC009761.287: 26902-27496	1.79769e+308			
MDP0000353412	MDC009761.287: 29079-29304	1.79769e+308			
MDP0000231304	MDC009798.251: 9799-13128	1.78051	AT2G33150.1	KAT2, PED1, PKT3	peroxisomal 3-ketoacyl-CoA thiolase 3
MDP0000239947	MDC009815.256: 8947-11799	2.62433	AT3G11180.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000292200	MDC009823.281: 1297-20823	1.79769e+308	AT3G01610.1	CDC48C, emb1354	cell division cycle 48C
MDP0000292200	MDC009823.281: 1297-20823	1.79769e+308	AT3G01610.1	CDC48C, emb1354	cell division cycle 48C
MDP0000287919	MDC009830.388: 12732-14292	1.79769e+308	AT5G13930.1	ATCHS, CHS, TT4	Chalcone and stilbene synthase family protein
0	MDC009830.388: 3008-4348	1.79769e+308	AT5G13930.1	CHS, TT4, ATCHS	Chalcone and stilbene synthase family protein
MDP0000703851	MDC009836.225: 17066-18219	2.31731	AT4G37300.1	MEE59	maternal effect embryo arrest 59
MDP0000850409	MDC009848.204: 8363-8600	-4.67506			
MDP0000125095	MDC009861.437: 3891-4319	-2.80388	AT5G38760.1		Late embryogenesis abundant protein (LEA) family protein
MDP0000291925	MDC009861.464: 1768-13770	-2.02662	AT5G38760.1		Late embryogenesis abundant protein (LEA) family protein
MDP0000187103	MDC009909.204: 5928-6981	1.79769e+308	AT5G67080.1	MAPKKK19	mitogen-activated protein kinase kinase kinase 19
MDP0000454694	MDC009933.158: 11532-19587	-2.20363	AT1G72820.1		Mitochondrial substrate carrier family protein
MDP0000125143	MDC009940.459: 13383-13777	1.79769e+308	AT2G19385.1		zinc ion binding
MDP0000287566	MDC009986.307: 3331-10534	2.41066	AT5G49230.1	HRB1	Drought-responsive family protein
MDP0000191667	MDC010015.212: 741-6386	2.23913	AT4G13430.1	ATLEUC1, IIL1	isopropyl malate isomerase large subunit 1
MDP0000289011	MDC010104.925: 5261-8066	2.73062	AT3G09270.1	ATGSTU8, GSTU8	glutathione S-transferase TAU 8
MDP0000285894	MDC010113.132: 1890-6718	1.79769e+308	AT5G53130.1	ATCNGC1, CNGC1	cyclic nucleotide gated channel 1
MDP0000645502	MDC010137.193: 5899-6763	1.79769e+308			
0	MDC010174.397: 1163-1411	1.79769e+308	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000909081	MDC010177.373: 8987-12973	3.00973	AT2G37790.1		NAD(P)-linked oxidoreductase superfamily protein
MDP0000776953	MDC010183.335: 5076-5272	1.79769e+308	AT5G63310.1	ATNDPK2, NDPK IA, NDPK IA IA, NDPK1A, NDPK2	nucleoside diphosphate kinase 2
MDP0000125336	MDC010195.886: 3529-4847	-3.53045	AT1G55260.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000777260	MDC010201.200: 11935-13257	1.6832	AT5G59530.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000138612	MDC010224.339: 7684-14666	1.79769e+308			
MDP0000116244	MDC010239.242: 2210-2815	3.42985	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000116244	MDC010239.242: 2917-3044	1.79769e+308	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000638442	MDC010241.223: 2599-3910	2.42596	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein
MDP0000188052	MDC010241.225: 11561-12807	2.52239	AT5G51970.1		GroES-like zinc-binding alcohol dehydrogenase family protein
MDP0000251295	MDC010246.430: 21589-22966	2.2344	AT1G05010.1	ACO4, EAT1, EFE	ethylene-forming enzyme
MDP0000125388	MDC010264.104: 2067-2797	1.79769e+308	AT5G35960.1		Protein kinase family protein
MDP0000668138	MDC010296.225: 19484-19807	1.79769e+308	AT3G52250.1		Duplicated homeodomain-like superfamily protein

MDP0000258062	MDC010332.272: 588-1152	1.79769e+308	AT5G10350.1		RNA-binding (RRM/RBD/RNP motifs) family protein
MDP0000233489	MDC010426.795: 7913-8261	1.79769e+308	AT5G48820.1	ICK6, KRP3	inhibitor/interactor with cyclin-dependent kinase
MDP0000292448	MDC010444.140: 7446-9204	-3.31146	AT5G38020.1		S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
MDP0000796596	MDC010462.160: 15024-15360	1.79769e+308			
MDP0000588940	MDC010473.396: 14867-15858	-3.86943	AT3G27200.1		Cupredoxin superfamily protein
0	MDC010474.340: 3456-4185	1.79769e+308	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
0	MDC010476.238: 18498-19659	4.06594	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000292131	MDC010476.238: 34773-35325	3.99199	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
0	MDC010507.323: 2408-2497	1.79769e+308			
MDP0000288622	MDC010541.240: 1517-3505	1.79769e+308	AT5G22860.1		Serine carboxypeptidase S28 family protein
MDP0000194046	MDC010550.498: 7035-7904	1.79769e+308	AT3G09270.1	ATGSTU8, GSTU8	glutathione S-transferase TAU 8
MDP0000566057	MDC010577.405: 11254-12570	1.79769e+308	AT2G36690.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000557646	MDC010584.403: 9855-16868	1.79769e+308	AT3G05500.1		Rubber elongation factor protein (REF)
0	MDC010589.234: 1224-1539	1.79769e+308			
MDP0000440922	MDC010598.348: 5127-6664	2.58806	AT5G36110.1	CYP716A1	cytochrome P450, family 716, subfamily A, polypeptide 1
MDP0000292176	MDC010630.204: 5140-5351	1.79769e+308	AT1G08450.1	AtCRT3, CRT3, EBS2, PSL1	calreticulin 3
MDP0000191951	MDC010729.433: 8183-8534	1.79769e+308			
MDP0000259250	MDC010764.217: 2450-4361	-2.08975	AT4G11220.1	BTI2, RTNLB2	VIRB2-interacting protein 2
MDP0000549056	MDC010870.164: 3469-9528	3.09695	AT1G68840.1	EDF2, RAP2.8, RAV2, TEM2	related to ABI3/VP1 2
0	MDC010876.313: 27953-28158	1.79769e+308			
0	MDC010912.583: 5714-6300	3.70536	AT2G36380.1	PDR6, ATPDR6	pleiotropic drug resistance 6
MDP0000893506	MDC010932.713: 30968-31739	1.79769e+308	AT1G68450.1		VQ motif-containing protein
MDP0000187492	MDC010968.194: 35563-43410	2.47873	AT2G26780.1		ARM repeat superfamily protein
0	MDC010981.245: 18382-19274	3.15585	AT3G61510.1	ACS1, AT-ACS1	ACC synthase 1
MDP0000289768	MDC011000.158: 4623-5925	1.79769e+308	AT3G23250.1	ATMYB15, ATY19, MYB15	myb domain protein 15
MDP0000126098	MDC011163.578: 6912-8415	1.79769e+308	AT5G20030.1		Plant Tudor-like RNA-binding protein
MDP0000188976	MDC011170.439: 2837-3077	1.79769e+308	AT2G15960.1		
MDP0000126152	MDC011264.166: 12266-14181	-2.83625	AT1G09575.1		Protein of unknown function (DUF607)
MDP0000880247	MDC011311.340: 11831-15202	2.41446	AT1G30755.1		Protein of unknown function (DUF668)
MDP0000906703	MDC011337.355: 7470-8262	-2.25482	AT3G59400.1	GUN4	enzyme binding;tetrapyrrole binding
0	MDC011359.150: 1008-1311	1.79769e+308			
0	MDC011372.235: 19894-20135	1.79769e+308			
MDP0000560179	MDC011400.321: 16471-19830	1.79769e+308	AT1G69370.1	cm-3, CM3	chorismate mutase 3
0	MDC011401.250: 14560-14880	-2.31808			
MDP0000138204	MDC011412.200: 2474-2656	1.79769e+308	AT1G01650.1	ATSPPL4, SPPL4	SIGNAL PEPTIDE PEPTIDASE-LIKE 4
MDP0000415910	MDC011412.206: 13093-13390	1.79769e+308	AT4G01840.1	ATKCO5, ATTPK5, KCO5, TPK5	Ca2+ activated outward rectifying K+ channel 5
MDP0000290114	MDC011437.437: 35717-37203	-2.74555	AT2G01770.1	ATVIT1, VIT1	vacuolar iron transporter 1
MDP0000031172	MDC011441.318: 5874-6624	1.79769e+308	AT4G38620.1	ATMYB4, MYB4	myb domain protein 4
0	MDC011449.97: 11886-12570	1.79769e+308	AT2G18680.1		unknown protein

MDP0000286168	MDC011456.83: 10260-11593	-2.17958	AT5G13490.1	AAC2	ADP/ATP carrier 2
0	MDC011459.391: 12253-12872	1.79769e+308	AT2G39210.1		Major facilitator superfamily protein
MDP0000361947	MDC011469.280: 8071-8371	3.5144			
MDP0000661951	MDC011469.280: 8412-12283	2.3818	AT4G11820.2	EMB2778, FKP1, HMGS, MVA1	hydroxymethylglutaryl-CoA synthase / HMG-CoA synthase / 3-hydroxy-3-methylglutaryl coenzyme A synthase
MDP0000902434	MDC011537.547: 10554-10740	1.79769e+308	AT4G05030.1		Copper transport protein family
MDP0000902434	MDC011537.547: 9633-10450	2.21998	AT4G05030.1		Copper transport protein family
0	MDC011542.145: 14812-15089	-2.78853			
MDP0000290254	MDC011554.266: 8335-11088	2.78301			
MDP0000185643	MDC011581.443: 34972-37559	-2.0884	AT1G70090.1	GATL9, LGT8	glucosyl transferase family 8
MDP0000185643	MDC011581.443: 34972-37559	1.79769e+308	AT1G70090.1	GATL9, LGT8	glucosyl transferase family 8
0	MDC011583.325: 5690-5843	1.79769e+308			
MDP0000150382	MDC011596.290: 3499-8925	2.75396	AT2G43820.1	ATSAGT1, GT, SAGT1, SGT1, UGT74F2	UDP-glucosyltransferase 74F2
0	MDC011598.529: 10860-11398	2.42453			
MDP0000926540	MDC011602.378: 2520-3183	1.88338	AT3G02430.1		Protein of unknown function (DUF679)
0	MDC011603.242: 16362-17137	1.86683	AT4G33720.1		CAP (Cysteine-rich secretory proteins, Antigen 5, and Pathogenesis-related 1 protein) superfamily protein
MDP0000199152	MDC011612.43: 0-3077	2.18079	AT4G16730.1	TPS02	terpene synthase 02
MDP0000139971	MDC011642.187: 6067-13143	2.14987	AT4G36710.1		GRAS family transcription factor
MDP0000126455	MDC011659.224: 3319-4725	-3.00214	AT1G10200.1	WLIM1	GATA type zinc finger transcription factor family protein
MDP0000292543	MDC011678.338: 3910-4160	1.79769e+308	AT3G22380.2	TIC	time for coffee
MDP0000251253	MDC011704.133: 11215-11348	1.79769e+308	AT1G76490.1	HMG1, HMGR1	hydroxy methylglutaryl CoA reductase 1
MDP0000771887	MDC011723.416: 11571-12015	-2.22297	AT1G60950.1	ATFD2, FED A	2Fe-2S ferredoxin-like superfamily protein
MDP0000328550	MDC011745.99: 15351-15722	-2.18845			
0	MDC011770.416: 7739-8412	2.51628	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
0	MDC011773.84: 2484-3065	5.81577	AT2G23270.1		unknown protein
MDP0000873235	MDC011784.207: 16-913	2.39345	AT3G54420.1	ATCHITIV, ATEP3, CHIV, EP3	homolog of carrot EP3-3 chitinase
MDP0000430546	MDC011784.298: 1990-4727	2.46989	AT3G54420.1	ATCHITIV, ATEP3, CHIV, EP3	homolog of carrot EP3-3 chitinase
MDP0000336546	MDC011792.236: 31818-38424	1.79769e+308	AT3G27460.1		SGF29 tudor-like domain
MDP0000672129	MDC011802.265: 2819-3744	-1.97863	AT3G26420.1	ATRZ-1A	RNA-binding (RRM/RBD/RNP motifs) family protein with retrovirus zinc finger-like domain
MDP0000618065	MDC011822.207: 10507-11080	1.79769e+308	AT3G11820.2	AT-SYR1, ATSYP121, ATSYR1, PEN1, SYP121, SYR1	syntaxin of plants 121
MDP0000416120	MDC011856.191: 7049-7379	1.79769e+308	AT4G27060.1	CN, SPR2, TOR1	ARM repeat superfamily protein
0	MDC011857.111: 12385-12818	-2.80994			
0	MDC011938.114: 11698-11941	1.79769e+308			
MDP0000259719	MDC011953.180: 21178-29290	2.13451	AT1G21480.1		Exostosin family protein
0	MDC011960.157: 14970-15370	1.79769e+308			

MDP0000203230	MDC011969.177: 1032-2423	5.0603	AT5G38940.1		RmlC-like cupins superfamily protein
MDP0000139824	MDC011983.274: 13866-23337	-2.1557	AT1G34630.1		
MDP0000342813	MDC011995.314: 7397-7948	1.79769e+308	AT2G23090.1		Uncharacterised protein family SERF
MDP0000576584	MDC011995.316: 6927-7232	1.79769e+308	AT5G64160.1		
MDP0000910523	MDC011998.433: 31142-33376	2.47451	AT5G05320.1		FAD/NAD(P)-binding oxidoreductase family protein
MDP0000647373	MDC012019.302: 8116-8353	1.79769e+308			
MDP0000140046	MDC012024.335: 4054-9352	2.79415	AT5G47770.1	FPS1	farnesyl diphosphate synthase 1
0	MDC012039.280: 32641-32933	1.79769e+308			
MDP0000750556	MDC012049.250: 246-726	3.88038	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000259661	MDC012049.376: 1086-2288	3.32901			
MDP0000418277	MDC012049.376: 7654-8475	4.23797			
MDP0000260110	MDC012049.377: 1467-1947	3.64793	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000611200	MDC012049.378: 11944-12424	4.45514	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000195614	MDC012049.378: 15381-15861	3.37256	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000293143	MDC012049.378: 7676-9891	3.59297	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000241271	MDC012083.378: 41-1721	-2.27036	AT3G06778.1		Chaperone DnaJ-domain superfamily protein
MDP0000152278	MDC012083.521: 11-527	4.0936	AT4G16740.1	ATTPS03, TPS03	terpene synthase 03
MDP0000126789	MDC012097.411: 814-2116	1.79769e+308	AT1G07230.1	NPC1	non-specific phospholipase C1
MDP0000233177	MDC012168.191: 14092-15547	-3.4026	AT1G10550.1	XET, XTH33	xyloglucan: xyloglucosyl transferase 33
MDP0000241358	MDC012226.83: 8174-8929	3.45922	AT1G74950.1	JAZ2, TIFY10B	TIFY domain/Divergent CCT motif family protein
MDP0000126892	MDC012245.148: 3093-3709	1.79769e+308	AT4G38060.2		
MDP0000295823	MDC012255.109: 11234-11389	1.79769e+308	AT5G20040.1	ATIPT9, IPT9	isopentenyltransferase 9
0	MDC012256.180: 17521-17661	1.79769e+308			
0	MDC012284.228: 14592-15163	3.41084			
MDP0000126954	MDC012310.593: 2815-3479	1.79769e+308			
0	MDC012310.599: 10117-10381	1.79769e+308			
MDP0000241432	MDC012341.121: 5328-14277	2.20523	AT1G60900.1		U2 snRNP auxilliary factor, large subunit, splicing factor
MDP0000126976	MDC012346.135: 2972-4484	-2.48248	AT2G33510.1		
0	MDC012355.316: 11597-11962	1.79769e+308			
MDP0000139052	MDC012379.228: 1791-2421	2.02621	AT4G20780.1	CML42	calmodulin like 42
0	MDC012392.481: 2083-2367	1.79769e+308	AT2G29420.1	ATGSTU7, GST25, GSTU7	glutathione S-transferase tau 7
0	MDC012392.481: 2550-3061	4.57808	AT3G09270.1	ATGSTU8, GSTU8	
MDP0000151934	MDC012402.49: 8557-11135	-2.01946	AT4G28850.1	ATXTH26, XTH26	xyloglucan endotransglucosylase/hydrolase 26
MDP0000294379	MDC012403.580: 3692-9461	3.59693	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000144836	MDC012403.589: 9512-9725	3.55338			
MDP0000201530	MDC012413.391: 9456-9744	1.79769e+308	AT5G14570.1	ATNRT2.7, NRT2.7	high affinity nitrate transporter 2.7
MDP0000152368	MDC012454.133: 870-5284	1.79769e+308	AT5G60370.1		
0	MDC012466.566: 156-300	1.79769e+308			
0	MDC012491.391: 15695-16226	-1.79382			

0	MDC012493.147: 8427-8656	1.79769e+308			
MDP0000609876	MDC012499.268: 30672-31306	5.56244	AT5G28640.1	AN3, ATGIF1, GIF, GIF1	SSXT family protein
MDP0000903805	MDC012506.282: 5827-8190	3.70347	AT1G73050.1		Glucose-methanol-choline (GMC) oxidoreductase family protein
MDP0000202716	MDC012509.602: 2756-6464	1.84839	AT2G41690.1	AT-HSFB3, HSFB3	heat shock transcription factor B3
MDP0000197764	MDC012535.429: 23420-31367	1.79769e+308	AT5G61450.1		P-loop containing nucleoside triphosphate hydrolases superfamily protein
MDP0000427172	MDC012537.136: 2027-2365	1.79769e+308	AT1G69060.1		Chaperone DnaJ-domain superfamily protein
MDP0000427172	MDC012537.136: 2472-3087	5.39463	AT1G69060.1		Chaperone DnaJ-domain superfamily protein
MDP0000648218	MDC012539.194: 16182-17073	1.9807	AT1G23710.1		Protein of unknown function (DUF1645)
MDP0000150727	MDC012578.402: 50168-50408	1.79769e+308	AT1G50500.1	ATVPS53, HIT1, VPS53	Membrane trafficking VPS53 family protein
MDP0000127122	MDC012582.369: 20321-21404	-1.95481	AT2G32300.1	UCC1	uclacyanin 1
MDP0000708928	MDC012593.380: 41318-42423	-3.50148	AT2G05070.1	LHCB2, LHCB2.2	photosystem II light harvesting complex gene 2.2
MDP0000152323	MDC012595.126: 7479-7658	1.79769e+308	AT3G22430.1		
MDP0000127134	MDC012597.1552: 1503-2265	3.29898	AT3G23240.1	ATERF1, ERF1	ethylene response factor 1
MDP0000205052	MDC012623.194: 30088-30799	1.79769e+308			
MDP0000300351	MDC012623.194: 31381-34645	1.79769e+308			
MDP0000197224	MDC012641.253: 15589-15898	1.9322			
MDP0000127185	MDC012660.72: 295-5944	1.79769e+308	AT5G14270.2	ATBET9, BET9	bromodomain and extraterminal domain protein 9
MDP0000334047	MDC012688.235: 31743-33240	3.21746	AT1G01720.1	ANAC002, ATAF1	NAC (No Apical Meristem) domain transcriptional regulator superfamily protein
0	MDC012696.212: 377-1037	1.91257			
MDP0000809488	MDC012716.217: 13456-14896	1.86079	AT4G27450.1		Aluminium induced protein with YGL and LRDR motifs
0	MDC012733.121: 11561-12529	1.79769e+308	AT4G11280.1	ACS6, ATACS6	1-aminocyclopropane-1-carboxylic acid (acc) synthase 6
MDP0000851204	MDC012735.249: 4715-5222	-1.89038	AT2G25770.1		Polyketide cyclase/dehydrase and lipid transport superfamily protein
MDP0000241694	MDC012816.263: 1287-2659	3.41245			
MDP0000299311	MDC012816.264: 988-1468	4.67582	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000295542	MDC012816.382: 14124-14604	5.13553	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000295543	MDC012816.382: 17333-17813	5.13278	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000814399	MDC012816.382: 20717-21197	4.71788	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000295540	MDC012816.382: 7552-8032	4.73806	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000294030	MDC012817.651: 4113-4501	1.79769e+308			
MDP0000127346	MDC012859.232: 2261-2690	1.79769e+308	AT5G16940.1		carbon-sulfur lyases
MDP0000364657	MDC012885.350: 14190-14436	-1.84875			
MDP0000470916	MDC012888.280: 16453-18375	2.25112	AT5G20230.1	ATBCB, BCB, SAG14	blue-copper-binding protein
MDP0000808076	MDC012888.280: 5525-6239	2.08673	AT5G20230.1	ATBCB, BCB, SAG14	blue-copper-binding protein
0	MDC012892.148: 4018-4407	1.79769e+308			
MDP0000155307	MDC012898.383: 1071-4451	-1.78424	AT5G66740.1		Protein of unknown function (DUF620)
0	MDC012900.215: 12407-12925	1.79769e+308	AT5G01710.1		methyltransferases
MDP0000879217	MDC012905.365: 22031-22294	1.79769e+308	AT5G58860.1	CYP86, CYP86A1	cytochrome P450, family 86, subfamily A, polypeptide 1
MDP0000260620	MDC012905.365: 5717-11456	-2.31112	AT2G29640.1	JOSL	JOSEPHIN-like protein
MDP0000241771	MDC012934.235: 1022-7184	1.97977	AT2G22250.2	AAT, ATAAT, MEE17	aspartate aminotransferase

MDP0000697676	MDC012951.271: 9076-10542	1.79769e+308	AT5G02230.1		Haloacid dehalogenase-like hydrolase (HAD) superfamily protein
MDP0000543204	MDC012957.285: 3141-3411	1.79769e+308			
MDP0000141463	MDC012987.400: 9772-11178	-3.00214	AT1G10200.1	WLIM1	GATA type zinc finger transcription factor family protein
MDP0000322416	MDC013003.189: 92143-92977	1.79769e+308	AT5G16360.1		NC domain-containing protein-related
MDP0000297138	MDC013044.213: 3080-8904	1.79769e+308	AT4G33580.1	ATBCA5, BCA5	beta carbonic anhydrase 5
MDP0000744506	MDC013064.706: 8737-8927	1.79769e+308	AT1G58050.1		RNA helicase family protein
MDP0000201700	MDC013070.55: 5428-5946	-4.65078	AT5G59845.1		Gibberellin-regulated family protein
MDP0000295655	MDC013084.249: 842-11955	1.79769e+308	AT5G39890.1		Protein of unknown function (DUF1637)
MDP0000198406	MDC013085.232: 856-1627	1.74151	AT4G03510.1	ATRMA1, RMA1	RING membrane-anchor 1
MDP0000943292	MDC013096.127: 30413-30872	3.16275	AT2G47485.1		
MDP0000298575	MDC013096.127: 5650-13638	1.79769e+308	AT1G68190.1		B-box zinc finger family protein
MDP0000298767	MDC013101.424: 1874-8337	1.79769e+308	AT5G13020.1		Emsy N Terminus (ENT)/ plant Tudor-like domains-containing protein
0	MDC013104.583: 2153-2490	1.79769e+308			
MDP0000391210	MDC013104.650: 7020-7701	1.79769e+308	AT5G06320.1	NHL3	NDR1/HIN1-like 3
MDP0000298031	MDC013115.223: 1700-1934	1.79769e+308	AT4G19210.1	ATRLI2, RLI2	RNAse l inhibitor protein 2
MDP0000297093	MDC013124.81: 6887-8992	-2.2894	AT3G02380.1	ATCOL2, COL2	CONSTANS-like 2
MDP0000775613	MDC013124.82: 36109-36537	-2.59035	AT5G38760.1		Late embryogenesis abundant protein (LEA) family protein
MDP0000729348	MDC013141.176: 13225-14599	1.79769e+308	AT3G48180.1		
MDP0000294360	MDC013237.128: 1097-2970	1.96755	AT1G72310.1	ATL3	RING/U-box superfamily protein
MDP0000746564	MDC013254.184: 20555-22846	1.79769e+308	AT5G28770.2	AtbZIP63, BZO2H3	bZIP transcription factor family protein
MDP0000231605	MDC013292.274: 11565-11880	4.44273	AT3G03560.1		
MDP0000770800	MDC013293.150: 1391-3136	4.58566	AT5G54160.1	ATOMT1, OMT1	O-methyltransferase 1
MDP0000552625	MDC013293.259: 4365-6445	1.79769e+308	AT5G54160.1	ATOMT1, OMT1	O-methyltransferase 1
MDP0000251667	MDC013317.553: 6374-6890	2.19849	AT3G53030.1	SRPK4	ser/arg-rich protein kinase 4
MDP0000297541	MDC013322.286: 4846-5170	-3.45586	AT4G10810.1		
MDP0000299310	MDC013323.310: 3368-3941	3.23961	AT5G37740.1		Calcium-dependent lipid-binding (CaLB domain) family protein
MDP0000509613	MDC013334.62: 6231-9119	2.82965	AT5G54500.1	FQR1	flavodoxin-like quinone reductase 1
0	MDC013340.296: 1896-2851	2.15177	AT5G66900.1		Disease resistance protein (CC-NBS-LRR class) family
MDP0000879254	MDC013370.129: 3544-3757	1.79769e+308	AT5G27740.1	EMB161, EMB251, EMB2775, RFC3	ATPase family associated with various cellular activities (AAA)
MDP0000321244	MDC013391.281: 2664-5545	-2.72681	AT2G39730.1	RCA	rubisco activase
MDP0000127750	MDC013396.400: 1704-2232	1.79769e+308	AT5G06280.1		
MDP0000781483	MDC013398.12: 1975-2220	1.79769e+308	AT5G05780.1	AE3, ATHMOV34, RPN8A	RP non-ATPase subunit 8A
0	MDC013436.578: 2-321	4.86954			
MDP0000197294	MDC013447.197: 2467-3134	-2.37931	AT1G59590.1	ZCF37	ZCF37
MDP0000330267	MDC013483.319: 9906-10138	1.79769e+308	AT1G51720.1		Amino acid dehydrogenase family protein
MDP0000242107	MDC013483.320: 693-11036	1.79769e+308	AT3G21295.1		Tudor/PWWP/MBT superfamily protein
MDP0000294034	MDC013503.290: 1841-10868	-3.89521	AT5G54490.1	PBP1	pinoid-binding protein 1
MDP0000202103	MDC013530.431: 3610-9556	2.12598	AT5G66680.1	DGL1	dolichyl-diphosphooligosaccharide-protein glycosyltransferase 48kDa subunit family protein

0	MDC013531.194: 13169-13505	-1.68373	AT3G54820.1	PIP2D, PIP2;5	plasma membrane intrinsic protein 2;5
MDP0000127858	MDC013560.287: 995-1943	2.54815	AT1G01550.1	BPS1	Protein of unknown function (DUF793)
MDP0000296782	MDC013694.297: 8575-9076	-2.08309	AT1G76100.1	PETE1	plastocyanin 1
MDP0000292511	MDC013737.149: 32341-48180	-2.49478	AT1G31280.1	AGO2	Argonaute family protein
MDP0000293269	MDC013748.450: 1014-3320	-2.4209	AT1G23740.1		Oxidoreductase, zinc-binding dehydrogenase family protein
0	MDC013772.153: 26501-26780	1.79769e+308			
MDP0000292908	MDC013792.490: 2156-2412	1.79769e+308	AT1G11300.1		protein serine/threonine kinases;protein kinases;ATP binding;sugar binding;kinases;carbohydrate binding
MDP0000613481	MDC013811.289: 959-1532	1.79769e+308	AT3G11820.2	AT-SYR1, ATSYP121, ATSYR1, PEN1, SYP121, SYR1	syntaxin of plants 121
0	MDC013818.335: 4169-4688	3.36997			
0	MDC013883.433: 28953-29243	1.79769e+308	AT2G27450.2	NLP1, ATNLP1, CPA	nitrilase-like protein 1
MDP0000852436	MDC013898.320: 3711-4586	1.93167	AT4G14305.1		Peroxisomal membrane 22 kDa (Mpv17/PMP22) family protein
MDP0000801806	MDC013941.232: 17328-17757	1.79769e+308	AT2G44310.1		Calcium-binding EF-hand family protein
MDP0000300051	MDC013941.240: 13812-14241	1.79769e+308	AT2G44310.1		Calcium-binding EF-hand family protein
0	MDC013941.240: 3518-4137	1.79769e+308			
0	MDC013955.368: 6283-6564	1.78501			
0	MDC013969.325: 6821-6931	1.79769e+308			
MDP0000321180	MDC013970.243: 6073-9465	-2.361	AT4G27310.1		B-box type zinc finger family protein
MDP0000328448	MDC013970.243: 6073-9465	-2.18489			
0	MDC014001.354: 28948-29441	3.47093			
MDP0000199273	MDC014010.337: 25823-32224	3.30595	AT1G70710.1	ATGH9B1, CEL1, GH9B1	glycosyl hydrolase 9B1
MDP0000232028	MDC014064.227: 18740-19212	1.79769e+308	AT4G14290.1		alpha/beta-Hydrolases superfamily protein
MDP0000299402	MDC014069.193: 12100-15622	1.96623	AT5G47770.1	FPS1	farnesyl diphosphate synthase 1
0	MDC014100.85: 6143-6452	1.79769e+308			
MDP0000259550	MDC014142.468: 6624-9069	-2.19289	AT3G23560.1	ALF5	MATE efflux family protein
0	MDC014145.337: 859-1071	1.79769e+308			
MDP0000934638	MDC014183.458: 6858-6948	1.79769e+308	AT1G68320.1	AtMYB62, BW62B, BW62C, MYB62	myb domain protein 62
MDP0000151848	MDC014188.335: 19493-19720	1.79769e+308	AT4G38960.3		B-box type zinc finger family protein
MDP0000151871	MDC014189.230: 15027-17751	1.79769e+308	AT5G63140.1	ATPAP29, PAP29	purple acid phosphatase 29
MDP0000380032	MDC015008.179: 340-1209	1.79769e+308	AT3G09270.1	ATGSTU8, GSTU8	glutathione S-transferase TAU 8
MDP0000296890	MDC015025.46: 19239-23920	4.28703	AT5G64010.1		
0	MDC015077.305: 4104-4809	1.79769e+308	AT2G45570.1	CYP76C2	cytochrome P450, family 76, subfamily C, polypeptide 2
MDP0000242554	MDC015092.88: 5088-9340	2.73401	AT1G32640.1	ATMYC2, JAI1, JIN1, MYC2, RD22BP1, ZBF1	Basic helix-loop-helix (bHLH) DNA-binding family protein
MDP0000128423	MDC015104.166: 2087-5923	2.28599	AT2G40095.1		Alpha/beta hydrolase related protein
MDP0000537361	MDC015142.537: 14989-16316	-1.39589	AT1G17890.1	GER2	NAD(P)-binding Rossmann-fold superfamily protein
0	MDC015146.108: 31720-32772	-1.98175	AT2G04780.2	FLA7	FASCICLIN-like arabinoogalactan 7
MDP0000141470	MDC015208.187: 15605-15861	1.79769e+308	AT1G17440.1	EER4, TAF12B	Transcription initiation factor TFIID subunit A

MDP0000199052	MDC015262.201: 26347-28858	1.79769e+308	AT3G12170.1		Chaperone DnaJ-domain superfamily protein
0	MDC015272.259: 4201-4401	1.79769e+308	AT3G02050.1	KUP3, ATKUP3, ATKT4	K+ uptake transporter 3
MDP0000886138	MDC015326.176: 6704-8094	3.222	AT2G41380.1		S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
MDP0000128562	MDC015329.200: 5868-6237	4.48568	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000292846	MDC015334.66: 31137-33830	-2.13953	AT3G12650.1		
MDP0000911067	MDC015370.131: 7512-9083	2.65117	AT5G36110.1	CYP716A1	cytochrome P450, family 716, subfamily A, polypeptide 1
MDP0000211411	MDC015465.154: 6369-6696	1.89734	AT2G46330.1	AGP16, ATAGP16	arabinogalactan protein 16
MDP0000643281	MDC015509.61: 3168-14885	1.90115	AT5G50230.1		Transducin/WD40 repeat-like superfamily protein
MDP0000804928	MDC015524.135: 32477-32885	2.39618	AT1G29290.1		
MDP0000211726	MDC015555.52: 35553-37271	-3.57441	AT3G25570.1		Adenosylmethionine decarboxylase family protein
0	MDC015568.269: 465-688	1.79769e+308			
MDP0000740648	MDC015573.110: 11769-12270	-2.10837	AT1G76100.1	PETE1	plastocyanin 1
MDP0000361550	MDC015573.110: 12297-12405	-2.18377			
MDP0000301453	MDC015614.99: 996-8975	2.76432	AT4G36760.1	APP1, ATAPP1	aminopeptidase P1
MDP0000926531	MDC015688.120: 16939-18822	1.79769e+308	AT5G55920.1	OLI2	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
0	MDC015710.110: 1669-1846	1.79769e+308			
MDP0000622590	MDC015714.239: 27931-31776	2.17217	AT2G41690.1	AT-HSFB3, HSFB3	heat shock transcription factor B3
MDP0000511014	MDC015753.354: 8942-11096	-2.69683			
0	MDC015771.323: 788-1107	1.79769e+308	AT1G31910.1		GHMP kinase family protein
MDP0000305934	MDC015800.101: 15993-16548	-1.96377	AT1G47960.1	ATC/VIF1, C/VIF1	cell wall / vacuolar inhibitor of fructosidase 1
MDP0000304497	MDC015808.251: 229-1821	-2.18938	AT5G38760.1		Late embryogenesis abundant protein (LEA) family protein
0	MDC015817.135: 987-1875	2.75131			
MDP0000207654	MDC015828.56: 17681-17876	1.79769e+308	AT2G20650.1		RING/U-box superfamily protein
MDP0000304369	MDC015831.96: 1977-2271	-2.01267	AT5G59320.1	LTP3	lipid transfer protein 3
MDP0000575586	MDC015856.331: 10564-10900	1.79769e+308	AT5G13640.1	ATPDAT, PDAT, PDAT1	phospholipid: diacylglycerol acyltransferase
MDP0000205889	MDC015861.207: 6372-7099	-3.13665	AT2G46330.1	AGP16, ATAGP16	arabinogalactan protein 16
MDP0000214320	MDC015872.319: 12837-13304	4.6241	AT5G42905.1		Polynucleotidyl transferase, ribonuclease H-like superfamily protein
0	MDC015872.319: 14910-15332	1.79769e+308			
MDP0000242922	MDC015883.197: 6246-9638	2.11224	AT5G25560.2		CHY-type/CTCHY-type/RING-type Zinc finger protein
0	MDC015908.225: 5190-5252	1.79769e+308			
MDP0000331516	MDC015921.316: 6350-6605	1.79769e+308			
MDP0000301675	MDC015929.425: 11804-12965	-1.185			
MDP0000304911	MDC015982.214: 20165-23127	1.79769e+308	AT3G26510.1		Octicosapeptide/Phox/Bem1p family protein
MDP0000641053	MDC016006.279: 2737-11176	-1.59982	AT5G64260.1	EXL2	EXORDIUM like 2
0	MDC016046.75: 14470-14707	1.79769e+308			
MDP0000920394	MDC016054.80: 4256-4514	1.8797	AT1G32928.1		
MDP0000140330	MDC016069.201: 7237-9538	1.79769e+308	AT2G43290.1	MSS3	Calcium-binding EF-hand family protein
MDP0000230446	MDC016069.206: 8663-10840	1.79769e+308	AT5G32440.3		Ubiquitin system component Cue protein
MDP0000307358	MDC016071.225: 7688-8061	1.79769e+308	AT5G64940.1	ATATH13, ATH13, ATOSA1, OSA1	ABC2 homolog 13

MDP0000603546	MDC016163.86: 1232-5672	3.30868	AT4G17880.1		Basic helix-loop-helix (bHLH) DNA-binding family protein
MDP0000150985	MDC016175.155: 5520-8899	1.79769e+308	AT1G80420.1	ATXRCC1	BRCT domain-containing DNA repair protein
0	MDC016234.268: 18791-19347	1.9365			
0	MDC016234.268: 19756-19922	1.79769e+308	AT5G07050.1		nodulin MtN21 /EamA-like transporter family protein
0	MDC016257.132: 1244-1326	1.79769e+308			
0	MDC016257.197: 16577-16693	2.51199			
MDP0000214905	MDC016257.212: 5600-8375	1.79769e+308	AT2G38740.1		Haloacid dehalogenase-like hydrolase (HAD) superfamily protein
MDP0000151417	MDC016323.148: 1566-3293	-3.48835	AT3G25570.1		Adenosylmethionine decarboxylase family protein
MDP0000348327	MDC016409.316: 14506-15265	-1.85887	AT1G12663.1		
MDP0000332786	MDC016470.67: 22850-23923	3.16876	AT5G04200.1	AtMC9, MC9	metacaspase 9
MDP0000332786	MDC016470.67: 24078-24292	1.79769e+308	AT5G04200.1	AtMC9, MC9	metacaspase 9
0	MDC016479.97: 23574-23802	1.79769e+308			
MDP0000432402	MDC016505.50: 1237-1427	1.79769e+308	AT5G38830.1		Cysteinyl-tRNA synthetase, class Ia family protein
MDP0000303139	MDC016572.135: 2036-13919	2.64572	AT5G13560.1		
0	MDC016588.101: 11842-12103	1.79769e+308			
MDP0000243237	MDC016615.207: 310-1511	1.79769e+308	AT5G17820.1		Peroxidase superfamily protein
MDP0000903267	MDC016626.388: 1735-2929	-1.99629	AT2G37400.1		Tetratricopeptide repeat (TPR)-like superfamily protein
0	MDC016663.136: 1192-1407	1.79769e+308			
MDP0000817718	MDC016670.201: 4492-4801	1.79769e+308	AT5G63610.1	ATCDK8, CDKE;1, HEN3	cyclin-dependent kinase E;1
MDP0000206461	MDC016676.357: 6049-7681	-2.02641	AT5G50790.1		Nodulin MtN3 family protein
0	MDC016716.178: 15966-16452	-1.91239			
0	MDC016737.160: 344-544	1.79769e+308			
0	MDC016762.98: 221-475	1.79769e+308			
MDP0000213265	MDC016787.195: 6612-9680	1.79769e+308	AT1G07960.1	ATPDIL5-1, PDIL5-1	PDI-like 5-1
MDP0000356415	MDC016842.248: 4052-4349	1.79769e+308			
MDP0000823528	MDC016855.631: 39541-39971	-1.94464	AT4G27360.1		Dynein light chain type 1 family protein
MDP0000828077	MDC016904.89: 2263-15477	2.31888	AT4G01470.1	ATTIP1.3, GAMMA-TIP3, TIP1;3	tonoplast intrinsic protein 1;3
MDP0000307237	MDC016920.355: 2401-4083	1.84566	AT3G21760.1	HYR1	UDP-Glycosyltransferase superfamily protein
MDP0000389969	MDC016942.263: 1081-4165	1.79769e+308	AT4G35260.1	IDH-I, IDH1	isocitrate dehydrogenase 1
MDP0000923628	MDC016948.79: 12312-12459	-1.87881	AT3G57062.1		
MDP0000213179	MDC016970.176: 123-435	-2.08908	AT5G65730.1	XTH6	xyloglucan endotransglucosylase/hydrolase 6
0	MDC017013.566: 1815-2228	1.79769e+308	AT2G45220.1		Plant invertase/pectin methylesterase inhibitor superfamily
0	MDC017013.566: 2346-2726	1.79769e+308	AT2G45220.1		Plant invertase/pectin methylesterase inhibitor superfamily
0	MDC017013.566: 514-1355	1.79769e+308	AT2G45220.1		Plant invertase/pectin methylesterase inhibitor superfamily
0	MDC017021.252: 20334-20684	1.79769e+308			
MDP0000304470	MDC017033.58: 322-2820	2.05019	AT3G66654.1		Cyclophilin-like peptidyl-prolyl cis-trans isomerase family protein
MDP0000307402	MDC017035.467: 27408-27827	3.77878	AT1G12650.1		
MDP0000234499	MDC017051.235: 13603-17570	2.02915	AT5G42260.1	BGLU12	beta glucosidase 12
MDP0000215541	MDC017065.233: 1015-1592	1.79769e+308			

MDP0000308097	MDC017091.105: 21457-21821	1.79769e+308	AT2G04220.1		Plant protein of unknown function (DUF868)
MDP0000507003	MDC017117.184: 9382-10816	2.94928	AT2G25060.1	AtENODL14, ENODL14	early nodulin-like protein 14
0	MDC017130.237: 1246-1897	4.57808	AT1G18390.2		Protein kinase superfamily protein
0	MDC017130.237: 652-870	1.79769e+308			
MDP0000252890	MDC017137.174: 6376-7583	-2.13152	AT5G38410.1		Ribulose bisphosphate carboxylase (small chain) family protein
MDP0000243529	MDC017153.343: 11521-14215	-2.09166	AT2G32670.1	ATVAMP725, VAMP725	vesicle-associated membrane protein 725
MDP0000513140	MDC017154.657: 12553-12769	1.79769e+308	AT1G51190.1	PLT2	Integrase-type DNA-binding superfamily protein
MDP0000351526	MDC017237.222: 14315-14834	-3.5073	AT2G45180.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000301189	MDC017251.289: 4484-5683	1.79769e+308	AT2G39490.1		F-box family protein
0	MDC017263.315: 11030-11368	1.79769e+308			
MDP0000233640	MDC017324.278: 8810-20137	7.32266	AT1G06720.1		P-loop containing nucleoside triphosphate hydrolases superfamily protein
MDP0000215301	MDC017325.138: 24398-26864	1.79769e+308	AT5G63060.1		Sec14p-like phosphatidylinositol transfer family protein
MDP0000755770	MDC017371.127: 20493-20837	1.79769e+308			
MDP0000755770	MDC017371.127: 21062-21293	1.79769e+308			
0	MDC017405.92: 18343-18890	-1.91427			
MDP0000302905	MDC017443.214: 7327-8900	1.79769e+308	AT5G13930.1	ATCHS, CHS, TT4	Chalcone and stilbene synthase family protein
0	MDC017450.136: 8789-9313	1.79769e+308	AT3G16340.2	PDR1	pleiotropic drug resistance 1
0	MDC017540.252: 44737-45439	1.79769e+308	AT4G20820.1		FAD-binding Berberine family protein
0	MDC017562.409: 111-463	2.33993			
MDP0000206473	MDC017564.90: 2113-2470	4.62132	AT1G51920.1		
MDP0000935120	MDC017578.59: 5707-6257	-2.69309	AT5G27670.1	HTA7	histone H2A 7
MDP0000696497	MDC017597.315: 14051-19216	2.53574	AT5G53110.1		RING/U-box superfamily protein
MDP0000214697	MDC017636.116: 4199-6265	2.00073	AT2G28690.1		Protein of unknown function (DUF1635)
0	MDC017703.193: 3608-3712	1.79769e+308			
MDP0000208899	MDC017766.81: 3875-5414	1.79769e+308	AT5G13930.1	ATCHS, CHS, TT4	Chalcone and stilbene synthase family protein
0	MDC017818.70: 8691-8779	1.79769e+308			
MDP0000130060	MDC017831.356: 6069-8826	1.79769e+308	AT5G54580.1		RNA-binding (RRM/RBD/RNP motifs) family protein
MDP0000208137	MDC017843.86: 131-1729	3.05473	AT1G56600.1	AtGolS2, GolS2	galactinol synthase 2
MDP0000492982	MDC017850.196: 7405-7687	1.79769e+308	AT3G53000.1	AtPP2-A15, PP2-A15	phloem protein 2-A15
MDP0000305335	MDC017850.205: 5561-9559	-1.74673	AT2G21990.1		Protein of unknown function, DUF617
MDP0000243861	MDC017880.286: 5763-5960	1.79769e+308	AT2G28930.3	APK1B, PK1B	protein kinase 1B
MDP0000708692	MDC017895.316: 14102-16075	1.79769e+308	AT2G38470.1	ATWRKY33, WRKY33	WRKY DNA-binding protein 33
0	MDC017935.299: 4662-5932	4.08189	AT1G30700.1		FAD-binding Berberine family protein
0	MDC018035.72: 1243-1306	-2.76812			
MDP0000261968	MDC018046.125: 72337-81764	3.09387	AT3G07790.1		DGCR14-related
MDP0000306151	MDC018097.432: 5006-5477	6.62325	AT2G23270.1		
0	MDC018101.293: 13762-13915	1.79769e+308	AT1G10010.1	AAP8, ATAAP8	amino acid permease 8
MDP0000792088	MDC018107.153: 10041-12319	2.51392	AT5G13080.1	ATWRKY75, WRKY75	WRKY DNA-binding protein 75

MDP0000302888	MDC018131.78: 74830-75020	1.79769e+308	AT2G40730.1		Protein kinase family protein with ARM repeat domain
MDP0000623836	MDC018185.243: 10459-11068	2.77536	AT3G21550.1	AtDMP2, DMP2	DUF679 domain membrane protein 2
0	MDC018197.265: 11208-11227	1.79769e+308			
MDP0000794439	MDC018238.148: 9565-11586	2.03383	AT1G80840.1	ATWRKY40, WRKY40	WRKY DNA-binding protein 40
MDP0000772208	MDC018262.284: 13539-14055	1.79769e+308	AT3G22560.1		Acyl-CoA N-acyltransferases (NAT) superfamily protein
MDP0000210067	MDC018268.357: 14874-17694	2.03795	AT2G14095.1		
MDP0000442718	MDC018328.126: 1463-1767	1.79769e+308	AT4G14145.1		
0	MDC018333.136: 493-815	1.79769e+308			
0	MDC018344.87: 12861-13103	1.79769e+308			
MDP0000307191	MDC018367.267: 12775-13673	4.45646	AT3G20840.1	PLT1	Integrase-type DNA-binding superfamily protein
0	MDC018370.363: 15975-16396	1.79769e+308			
0	MDC018385.173: 5099-5375	1.79769e+308			
MDP0000307797	MDC018389.342: 13517-13812	2.72922	AT1G23880.1		NHL domain-containing protein
MDP0000244125	MDC018407.210: 85-6962	1.79769e+308	AT1G01710.1		Acyl-CoA thioesterase family protein
MDP0000130449	MDC018419.403: 1052-2613	1.87905	AT5G36110.1	CYP716A1	cytochrome P450, family 716, subfamily A, polypeptide 1
MDP0000689946	MDC018430.130: 8323-8938	2.19853	AT5G47220.1	ATERF-2, ATERF2, ERF2	ethylene responsive element binding factor 2
MDP0000152589	MDC018440.197: 73746-74343	-3.28078	AT5G52190.1		Sugar isomerase (SIS) family protein
MDP0000341297	MDC018445.308: 1656-1818	1.79769e+308			
0	MDC018495.75: 656-1593	2.5651	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000950987	MDC018501.311: 3908-4131	1.79769e+308	AT4G03510.1	ATRMA1, RMA1	RING membrane-anchor 1
MDP0000212954	MDC018507.307: 11511-11932	1.79769e+308	AT1G70670.1		Caleosin-related family protein
MDP0000789174	MDC018519.270: 6935-7074	2.55974	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000569487	MDC018527.183: 1987-3563	1.79769e+308			
0	MDC018532.136: 875-1203	1.79769e+308	AT4G25340.2	FKBP53	FK506 BINDING PROTEIN 53
MDP0000664781	MDC018583.121: 765-1006	1.79769e+308	AT1G72040.1		P-loop containing nucleoside triphosphate hydrolases superfamily protein
MDP0000210867	MDC018599.370: 2113-2425	1.79769e+308			
MDP0000260882	MDC018600.265: 28896-33820	1.97082			
MDP0000207774	MDC018610.106: 7849-8953	-1.84235	AT3G20820.1		Leucine-rich repeat (LRR) family protein
MDP0000300795	MDC018638.210: 32468-32798	1.79769e+308	AT1G76710.1	ASHH1, SDG26	SET domain group 26
0	MDC018683.391: 5370-5442	1.79769e+308			
MDP0000206239	MDC018755.93: 19644-21164	-2.26016	AT2G18840.1		Integral membrane Yip1 family protein
0	MDC018763.284: 10-79	1.79769e+308			
MDP0000255006	MDC018763.300: 9907-13402	1.79769e+308	AT3G01720.1		
MDP0000302206	MDC018797.53: 4472-4733	-2.17361			
0	MDC018803.242: 11-340	2.78501			
MDP0000306963	MDC018808.231: 3422-3614	1.79769e+308	AT1G09630.1	ATRAB-A2A, ATRAB11C, ATRABA2A, RAB-A2A, RAB11c	RAB GTPase 11C
MDP0000523487	MDC018812.251: 54-3502	1.93781	AT3G55120.1	A11, CFI, TT5	Chalcone-flavanone isomerase family protein
MDP0000782882	MDC018829.211: 2566-3010	2.05088			

0	MDC018858.178: 25373-25918	2.18952	AT1G01490.2		Heavy metal transport/detoxification superfamily protein
0	MDC018858.178: 4311-4783	1.79769e+308			
MDP0000304278	MDC018864.196: 3981-5846	1.79769e+308	AT3G52040.1		
MDP0000130738	MDC018913.57: 3010-3796	1.79769e+308	AT1G68450.1		VQ motif-containing protein
MDP0000215667	MDC018916.143: 5252-7355	1.79769e+308			
MDP0000210595	MDC018926.465: 13230-16290	2.28894	AT1G03110.1		Transducin/WD40 repeat-like superfamily protein
MDP0000304459	MDC018926.465: 829-2636	1.49662	AT3G22550.1		Protein of unknown function (DUF581)
MDP0000211459	MDC018944.121: 6482-6638	1.79769e+308	AT1G19850.1	ARF5, IAA24, MP	Transcriptional factor B3 family protein / auxin-responsive factor AUX/IAA-related
MDP0000921319	MDC018952.103: 18323-18583	-4.80994	AT2G10940.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000921319	MDC018952.103: 19128-19710	-4.48923	AT2G10940.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000210434	MDC018952.103: 6545-13697	1.79769e+308	AT5G35430.1		Tetratricopeptide repeat (TPR)-like superfamily protein
MDP0000396298	MDC018995.219: 2843-3681	1.80436	AT1G80940.1		
0	MDC019060.82: 24775-25363	2.10784	AT1G01490.2		Heavy metal transport/detoxification superfamily protein
MDP0000207192	MDC019069.72: 1250-2242	2.34966	AT4G14305.1		Peroxisomal membrane 22 kDa (Mpv17/PMP22) family protein
MDP0000386314	MDC019073.253: 5201-5696	3.20804	AT4G25900.1		Galactose mutarotase-like superfamily protein
MDP0000386314	MDC019073.253: 5757-13541	1.79769e+308	AT4G25900.1		Galactose mutarotase-like superfamily protein
MDP0000303781	MDC019089.170: 15740-41193	2.27879	AT1G15740.1		Leucine-rich repeat family protein
MDP0000253234	MDC019095.61: 11627-11992	2.71134	AT5G64420.1		DNA polymerase V family
0	MDC019105.344: 1605-2183	1.79769e+308	AT4G23160.1	CRK8	cysteine-rich RLK (RECEPTOR-like protein kinase) 8
MDP0000358789	MDC019115.110: 2266-2740	-2.58413			
0	MDC019132.134: 222-374	1.79769e+308			
MDP0000365923	MDC019144.167: 7606-7891	1.79769e+308	AT5G27430.1		Signal peptidase subunit
MDP0000336695	MDC019148.87: 3921-4512	-4.33325	AT4G39250.1	ATRL1, RL1, RSM2	RAD-like 1
0	MDC019150.106: 626-852	1.85283			
MDP0000936735	MDC019171.140: 19104-20870	1.79769e+308	AT5G27410.2		D-aminoacid aminotransferase-like PLP-dependent enzymes superfamily protein
MDP0000321110	MDC019210.287: 8349-16802	1.79769e+308	AT5G06550.1		
MDP0000837139	MDC019255.177: 10423-10792	1.79769e+308	AT3G07340.1		basic helix-loop-helix (bHLH) DNA-binding superfamily protein
MDP0000827820	MDC019270.183: 15826-16306	4.71788	AT1G24020.1	MLP423	MLP-like protein 423
0	MDC019296.227: 19299-19915	-1.86788			
0	MDC019305.85: 5690-5943	1.79769e+308			
MDP0000143208	MDC019350.189: 9254-9462	1.79769e+308	AT5G08130.2	BIM1	basic helix-loop-helix (bHLH) DNA-binding superfamily protein
MDP0000222184	MDC019388.422: 2997-5399	1.79769e+308	AT5G36930.2		Disease resistance protein (TIR-NBS-LRR class) family
MDP0000508081	MDC019411.248: 5935-6349	1.79769e+308	AT2G44310.1		Calcium-binding EF-hand family protein
MDP0000696624	MDC019411.260: 1762-2191	1.79769e+308	AT2G44310.1		Calcium-binding EF-hand family protein
MDP0000310308	MDC019445.155: 6053-6213	1.79769e+308	AT2G06000.1		Pentatricopeptide repeat (PPR) superfamily protein
MDP0000322237	MDC019493.102: 3700-11010	1.79769e+308	AT5G54570.1	BGLU41	beta glucosidase 41
MDP0000329499	MDC019532.134: 17322-17472	1.79769e+308			
MDP0000880838	MDC019575.15: 12756-12778	2.06399	AT1G73740.1		UDP-Glycosyltransferase superfamily protein

MDP0000261679	MDC019580.344: 3704-9984	3.62236	AT5G26340.1	ATSTP13, MSS1, STP13	Major facilitator superfamily protein
0	MDC019583.195: 2352-2815	2.75015	AT2G37760.1		NAD(P)-linked oxidoreductase superfamily protein
0	MDC019583.195: 3051-3246	2.41451	AT2G37770.2		NAD(P)-linked oxidoreductase superfamily protein
MDP0000449901	MDC019585.197: 5928-6189	2.48902	AT1G19900.1		glyoxal oxidase-related protein
MDP0000449901	MDC019585.197: 6197-7127	1.92507	AT1G19900.1		glyoxal oxidase-related protein
MDP0000315936	MDC019603.257: 26665-27463	1.79769e+308	AT4G24990.1	ATGP4	Ubiquitin family protein
MDP0000311438	MDC019656.167: 25590-27856	1.79769e+308	AT2G03620.1	MGT3, MRS2-5	magnesium transporter 3
MDP0000218810	MDC019661.283: 3325-4682	4.53059	AT4G10490.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
0	MDC019710.194: 14070-14423	2.21243			
MDP0000244775	MDC019719.227: 864-1022	1.79769e+308	AT2G19330.1	PIRL6	plant intracellular ras group-related LRR 6
MDP0000230601	MDC019748.161: 5809-7542	-2.15226	AT1G19000.1		Homeodomain-like superfamily protein
0	MDC019868.260: 1962-2259	1.79769e+308			
MDP0000218699	MDC019885.322: 5870-6995	2.2786	AT1G75800.1		Pathogenesis-related thaumatin superfamily protein
MDP0000632432	MDC019999.234: 2519-2972	-2.69166	AT4G14890.1		2Fe-2S ferredoxin-like superfamily protein
MDP0000593249	MDC020032.306: 1846-8801	-1.28641	AT2G32300.1	UCC1	uclacyanin 1
0	MDC020082.132: 384-673	1.79769e+308			
0	MDC020082.224: 15608-15824	1.79769e+308	AT1G66950.1	PDR11, ATPDR11	pleiotropic drug resistance 11
0	MDC020082.224: 16228-16490	1.79769e+308	AT2G36380.1	PDR6, ATPDR6	pleiotropic drug resistance 6
0	MDC020082.224: 16703-17360	5.93328	AT2G36380.1	PDR6, ATPDR6	pleiotropic drug resistance 6
0	MDC020098.119: 12808-13292	1.79769e+308	AT3G16340.2	PDR1	pleiotropic drug resistance 1
MDP0000412490	MDC020101.37: 12007-12985	-3.44931	AT1G56430.1	ATNAS4, NAS4	nicotianamine synthase 4
MDP0000357039	MDC020112.161: 5075-5343	1.79769e+308			
MDP0000705053	MDC020153.98: 3860-4787	2.38023	AT1G48320.1		Thioesterase superfamily protein
MDP0000705053	MDC020153.98: 5120-5424	1.79769e+308	AT1G48320.1		Thioesterase superfamily protein
MDP0000805832	MDC020185.100: 13522-14211	-2.15482	AT5G08050.1		Protein of unknown function (DUF1118)
0	MDC020190.132: 475-670	1.79769e+308			
MDP0000312316	MDC020206.60: 19611-29042	6.42087	AT1G10510.1	emb2004	RNI-like superfamily protein
0	MDC020206.60: 80379-80919	3.66853	AT3G48180.1		unknown protein
MDP0000362305	MDC020215.147: 7355-7948	-1.80632	AT2G02100.1	LCR69, PDF2.2	low-molecular-weight cysteine-rich 69
MDP0000253928	MDC020235.551: 5712-6463	-1.97256	AT5G64820.1		
MDP0000351308	MDC020252.154: 3698-3890	1.79769e+308			
MDP0000745504	MDC020314.68: 30613-30835	1.79769e+308	AT1G02630.1		Nucleoside transporter family protein
MDP0000593536	MDC020317.187: 1475-2264	3.7415	AT2G36690.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000322725	MDC020357.143: 7538-13113	1.98536	AT4G29010.1	AIM1	Enoyl-CoA hydratase/isomerase family
0	MDC020381.113: 1718-2064	1.79769e+308			
MDP0000219404	MDC020461.201: 992-1634	-3.43143	AT3G22142.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000366807	MDC020476.369: 154-1663	2.415			
MDP0000920189	MDC020483.205: 11374-11570	1.79769e+308	AT3G23150.1	ETR2	Signal transduction histidine kinase, hybrid-type, ethylene sensor
MDP0000356161	MDC020502.79: 5346-6108	1.79769e+308	AT3G29970.1		B12D protein

MDP0000356161	MDC020502.79: 6418-6639	1.79769e+308	AT3G29970.1		B12D protein
MDP0000392904	MDC020542.316: 6274-6781	-1.89038	AT2G25770.1		Polyketide cyclase/dehydrase and lipid transport superfamily protein
MDP0000131822	MDC020582.164: 1549-3880	1.79769e+308	AT4G05100.1	AtMYB74, MYB74	myb domain protein 74
MDP0000827665	MDC020641.127: 10915-12751	-1.90145	AT5G41080.1		PLC-like phosphodiesterases superfamily protein
MDP0000353639	MDC020660.55: 9642-9750	1.79769e+308			
MDP0000831481	MDC020665.117: 6027-6473	2.9494	AT5G14280.1		DNA-binding storekeeper protein-related
MDP0000218132	MDC020684.226: 11654-14980	1.79769e+308	AT3G15070.1		RING/U-box superfamily protein
MDP0000472203	MDC020837.138: 583-9198	2.24942	AT5G18600.1		Thioredoxin superfamily protein
MDP0000311115	MDC020959.82: 16235-16669	1.79769e+308	AT5G51270.1		U-box domain-containing protein kinase family protein
0	MDC020997.87: 1778-2245	1.79769e+308			
MDP0000215799	MDC021014.157: 400-4861	1.79769e+308	AT1G50030.2	TOR	target of rapamycin
0	MDC021041.235: 4758-5058	1.79769e+308			
MDP0000143860	MDC021083.97: 4312-4666	1.79769e+308	AT4G15475.1		F-box/RNI-like superfamily protein
MDP0000314632	MDC021107.66: 19990-21331	-2.88031	AT1G70760.1	CRR23	inorganic carbon transport protein-related
MDP0000217690	MDC021125.222: 2795-2956	1.79769e+308	AT2G35980.1	ATNHL10, NHL10, YLS9	Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000758237	MDC021125.354: 16615-17911	3.56375	AT5G01750.2		Protein of unknown function (DUF567)
MDP0000312359	MDC021195.261: 14143-15009	2.1252	AT2G16060.1	AHB1, ARATH GLB1, ATGLB1, GLB1, HB1, NSHB1	hemoglobin 1
0	MDC021221.287: 44679-45111	2.02561			
MDP0000312258	MDC021224.329: 17770-36527	1.79769e+308	AT1G79000.1	ATHAC1, ATHPCAT2, HAC1, PCAT2	histone acetyltransferase of the CBP family 1
MDP0000312256	MDC021224.329: 4725-8465	1.27257	AT5G38630.1	ACYB-1, CYB-1	cytochrome B561-1
MDP0000225981	MDC021229.327: 8915-15234	1.79769e+308	AT3G45300.1	ATIVD, IVD, IVDH	isovaleryl-CoA-dehydrogenase
MDP0000313786	MDC021262.50: 13957-14057	1.79769e+308	AT3G15880.2	TPR4, WSIP2	WUS-interacting protein 2
MDP0000222305	MDC021270.197: 3504-5232	1.79769e+308	AT5G06710.1	HAT14	homeobox from Arabidopsis thaliana
MDP0000221246	MDC021379.127: 3832-9589	1.79769e+308	AT1G02840.1	ATSRP34, SR1, SRP34	RNA-binding (RRM/RBD/RNP motifs) family protein
MDP0000332721	MDC021386.436: 29757-30095	1.79769e+308			
MDP0000261935	MDC021421.104: 11161-11618	2.97142	AT5G27460.1		Tetratricopeptide repeat (TPR)-like superfamily protein
MDP0000217124	MDC021463.474: 2997-5056	1.79769e+308	AT1G77930.1		Chaperone DnaJ-domain superfamily protein
MDP0000142814	MDC021508.119: 703-1183	2.05401	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000314223	MDC021521.150: 23479-23682	-2.38109	AT1G78610.1	MSL6	mechanosensitive channel of small conductance-like 6
MDP0000336734	MDC021527.347: 5167-5551	-2.40514			
0	MDC021555.260: 3534-3862	1.79769e+308	AT4G20970.1		basic helix-loop-helix (bHLH) DNA-binding superfamily protein
0	MDC021563.286: 640-1084	2.21243	AT5G37850.3	SOS4	pfkB-like carbohydrate kinase family protein
MDP0000221871	MDC021563.301: 16401-23355	2.03305	AT5G37850.1	ATSOS4, SOS4	pfkB-like carbohydrate kinase family protein
0	MDC021594.146: 14-493	4.97147			
MDP0000315449	MDC021648.178: 15444-17993	1.79769e+308	AT2G26070.1	RTE1	Protein of unknown function (DUF778)
0	MDC021658.157: 9449-9957	-2.16656	AT1G60950.1	FED A, ATFD2	2Fe-2S ferredoxin-like superfamily protein
MDP0000392201	MDC021684.90: 873-4447	-2.20956	AT3G20820.1		Leucine-rich repeat (LRR) family protein

MDP0000313454	MDC021689.441: 3963-4557	5.51402	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000312569	MDC021689.443: 9371-9851	4.3114	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000216907	MDC021689.444: 11887-12520	4.4464	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000500806	MDC021689.444: 7604-11877	1.79769e+308	AT1G24020.1	MLP423	MLP-like protein 423
MDP0000576126	MDC021691.154: 2961-7337	-3.79609	AT5G38020.1		S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
MDP0000314777	MDC021716.303: 5439-6015	3.25986	AT3G21550.1	AtDMP2, DMP2	DUF679 domain membrane protein 2
MDP0000313600	MDC021763.143: 53-1175	2.44885	AT4G37300.1	MEE59	maternal effect embryo arrest 59
MDP0000764876	MDC021795.40: 6148-6790	-3.43143	AT3G22142.1		Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein
MDP0000542944	MDC021813.304: 19401-20097	-1.88806	AT3G22840.1	ELIP, ELIP1	Chlorophyll A-B binding family protein
MDP0000132431	MDC021842.102: 1393-3748	-2.43746	AT4G03210.1	XTH9	xyloglucan endotransglucosylase/hydrolase 9
MDP0000378203	MDC021843.194: 2520-4873	-2.1428	AT4G03210.1	XTH9	xyloglucan endotransglucosylase/hydrolase 9
MDP0000132456	MDC021864.218: 7479-8925	1.89573	AT5G42650.1	AOS, CYP74A, DDE2	allene oxide synthase
MDP0000574556	MDC021880.120: 18168-18768	2.77916	AT5G39670.1		Calcium-binding EF-hand family protein
MDP0000142675	MDC021907.185: 4850-5618	1.79769e+308			
MDP0000361589	MDC021912.336: 80015-80513	-2.59832	AT3G45980.1	H2B, HTB9	Histone superfamily protein
MDP0000309694	MDC021925.357: 9645-18947	2.03349	AT4G34640.1	ERG9, SQS1	squalene synthase 1
MDP0000312665	MDC021956.140: 17630-30598	1.79769e+308	AT5G06600.1	UBP12	ubiquitin-specific protease 12
MDP0000701077	MDC022002.79: 2723-4463	-2.10433	AT1G05850.1	ATCTL1, CTL1, ELP, ELP1, ERH2, HOT2, POM1	Chitinase family protein
MDP0000245720	MDC022027.142: 3660-5484	1.79769e+308	AT1G52800.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000261346	MDC022047.116: 7935-11907	-3.22425	AT2G28900.1	ATOEP16-1, ATOEP16-L, OEP16, OEP16-1	outer plastid envelope protein 16-1
MDP0000219282	MDC022049.136: 3911-5363	-3.07805	AT3G16520.3	UGT88A1	UDP-glucosyl transferase 88A1
MDP0000216076	MDC022049.144: 1863-2445	-2.6847	AT3G16520.3	UGT88A1	UDP-glucosyl transferase 88A1
0	MDC022084.259: 9269-9540	1.79769e+308			
0	MDC022115.179: 2130-2784	1.76737	AT5G06320.1	NHL3	NDR1/HIN1-like 3
MDP0000245757	MDC022126.96: 1332-1713	3.46619	AT1G72960.1		Root hair defective 3 GTP-binding protein (RHD3)
MDP0000309512	MDC022131.36: 462-5980	1.79769e+308	AT5G03290.1	IDH-V	isocitrate dehydrogenase V
MDP0000388769	MDC022151.329: 5891-9309	2.43417	AT2G37040.1	ATPAL1, PAL1	PHE ammonia lyase 1
MDP0000132621	MDC022159.201: 1198-1649	4.00098	AT5G43580.1		Serine protease inhibitor, potato inhibitor I-type family protein
MDP0000699845	MDC022200.129: 11651-13693	1.90489			
MDP0000309382	MDC022203.80: 8540-9550	2.21842	AT5G13180.1	ANAC083, NAC083, VNI2	NAC domain containing protein 83
MDP0000223410	MDC022295.98: 32919-34391	1.79769e+308	AT5G25170.1		PPPDE putative thiol peptidase family protein
MDP0000940098	MDC022297.232: 13220-15870	-2.69487	AT3G11910.1	UBP13	ubiquitin-specific protease 13
MDP0000328060	MDC022301.307: 90-353	1.79769e+308	AT5G61510.1		GroES-like zinc-binding alcohol dehydrogenase family protein
0	MDC022363.241: 6084-6289	1.79769e+308			
0	MDC022366.63: 24207-24828	3.6344	AT5G13220.4		jasmonate-zim-domain protein 10
0	MDC022366.63: 25851-26449	3.55241			
MDP0000366309	MDC022435.108: 200-507	1.79769e+308	AT1G05120.1		Helicase protein with RING/U-box domain

MDP0000372061	MDC022441.31: 99-976	2.95152	AT5G66170.3	STR18	sulfurtransferase 18
MDP0000370937	MDC022441.35: 130-1007	3.18225	AT5G66170.3	STR18	sulfurtransferase 18
MDP0000094255	MDC022474.98: 3860-12957	-2.186	AT1G04820.1	TOR2, TUA4	tubulin alpha-4 chain
MDP0000094255	MDC022474.98: 3860-12957	-2.1253	AT1G04820.1	TOR2, TUA4	tubulin alpha-4 chain
MDP0000656154	MDC022487.75: 10821-11616	-1.97446	AT2G34430.1	LHB1B1, LHCB1.4	light-harvesting chlorophyll-protein complex II subunit B1
MDP0000656152	MDC022487.75: 8161-8959	-1.86434	AT1G29930.1	AB140, CAB1, CAB140, LHCB1.3	chlorophyll A/B binding protein 1
0	MDC022531.114: 4018-4893	3.36846	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
0	MDC022564.61: 3605-3774	1.79769e+308			
MDP0000591411	MDC022569.33: 5324-5484	-3.41737	AT3G63380.1		ATPase E1-E2 type family protein / haloacid dehalogenase-like hydrolase family protein
MDP0000805894	MDC022597.70: 34733-36744	-2.17549	AT1G11860.1		Glycine cleavage T-protein family
MDP0000465139	MDC022631.45: 303-972	1.79769e+308	AT5G65310.1	ATHB-5, ATHB5, HB5	homeobox protein 5
MDP0000315498	MDC022702.107: 16118-17225	-3.11467	AT3G12610.1	DRT100	Leucine-rich repeat (LRR) family protein
MDP0000092978	MDC022773.244: 7871-8075	1.79769e+308	AT5G65290.1		LMBR1-like membrane protein
0	MDC022780.65: 594-837	2.55647			
MDP0000132952	MDC022792.139: 8367-9744	1.79769e+308	AT5G47980.1		HXXXD-type acyl-transferase family protein
MDP0000246042	MDC022803.121: 4647-6548	1.79769e+308	AT3G17600.1	IAA31	indole-3-acetic acid inducible 31
MDP0000254473	MDC022821.76: 29441-58233	1.9116	AT4G33680.1	AGD2	Pyridoxal phosphate (PLP)-dependent transferases superfamily protein
MDP0000225360	MDC022824.304: 3660-3829	1.79769e+308	AT4G26140.1	BGAL12	beta-galactosidase 12
MDP0000225483	MDC022839.109: 16313-16652	1.79769e+308	AT3G03860.1	APRL5, ATAPRL5	APR-like 5
0	MDC022879.56: 1375-1884	1.79769e+308	AT2G22420.1		Peroxidase superfamily protein
MDP0000308875	MDC022879.64: 8443-8780	1.79769e+308	AT5G10360.1	EMB3010, RPS6B	Ribosomal protein S6e
0	MDC022894.374: 9989-10324	1.79769e+308			
MDP0000145050	MDC023085.39: 1191-3316	1.79769e+308	AT2G31180.1	ATMYB14, MYB14, MYB14AT	myb domain protein 14
MDP0000154734	MDC023147.45: 4964-7678	2.37369	AT5G13080.1	ATWRKY75, WRKY75	WRKY DNA-binding protein 75
MDP0000144280	MDC023306.53: 6102-7273	1.79769e+308	AT1G35210.1		
MDP0000344130	MDC023311.35: 7749-8338	1.72265			
MDP0000655939	MDC023492.75: 33-679	3.53624	AT3G54420.1	ATCHITIV, ATEP3, CHIV, EP3	homolog of carrot EP3-3 chitinase
MDP0000310109	MDC023507.55: 3458-7466	2.57308	AT4G01560.1	MEE49	Ribosomal RNA processing Brix domain protein
MDP0000824468	MDC023572.35: 3291-4882	1.79769e+308	AT1G02120.1	VAD1	GRAM domain family protein
0	MDC023576.93: 1279-1667	-2.75104			
MDP0000769652	MDC023607.46: 9470-10046	4.48219	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000229468	MDC023757.22: 743-2304	2.00331	AT5G36110.1	CYP716A1	cytochrome P450, family 716, subfamily A, polypeptide 1
MDP0000767063	MDC023849.16: 6797-7283	1.79769e+308	AT1G35210.1		
MDP0000390049	MDC023913.71: 5802-6066	2.65704	AT1G34060.1		Pyridoxal phosphate (PLP)-dependent transferases superfamily protein
MDP0000254078	MDC024051.25: 30601-30826	1.79769e+308	AT5G63080.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000316310	MDC024251.13: 2237-3536	2.97323	AT1G78860.1		D-mannose binding lectin protein with Apple-like carbohydrate-binding domain
MDP0000254057	MDC024467.18: 10070-10976	1.79769e+308	AT2G27770.1		Plant protein of unknown function (DUF868)

0	MDC024785.32: 20131-20658	1.79769e+308			
MDP0000229958	MDC025025.28: 2836-3810	-4.49642	AT5G15230.1	GASA4	GAST1 protein homolog 4
MDP0000226405	MDC025032.16: 6902-7125	1.79769e+308	AT1G02400.1	ATGA2OX4, ATGA2OX6, DTA1, GA2OX6	gibberellin 2-oxidase 6
MDP0000316472	MDC025128.19: 896-2663	1.79769e+308			
0	MDC025179.21: 23-403	1.79769e+308			
MDP0000226193	MDC025338.53: 10778-16491	1.79769e+308	AT5G50400.1	ATPAP27, PAP27	purple acid phosphatase 27
0	MDC025463.22: 3749-4156	-3.07297			
MDP0000318256	MDC025619.11: 2890-10293	1.79769e+308	AT1G73050.1		Glucose-methanol-choline (GMC) oxidoreductase family protein
MDP0000318069	MDC025702.20: 9270-10841	2.65117	AT5G36110.1	CYP716A1	cytochrome P450, family 716, subfamily A, polypeptide 1
0	MDC026144.28: 2897-3346	-1.97344			
MDP0000229338	MDC026688.7: 88-304	2.13927	AT5G36110.1	CYP716A1	cytochrome P450, family 716, subfamily A, polypeptide 1
MDP0000316181	MDC027100.17: 2364-7236	1.79769e+308	AT1G51740.1	ATSYP81, ATUFE1, SYP81, UFE1	syntaxin of plants 81
MDP0000133520	MDC027330.53: 6528-8747	1.79769e+308	AT2G26560.1	PLA IIA, PLA2A, PLP2	phospholipase A 2A
MDP0000228673	MDC027343.22: 8537-10521	-1.88286	AT5G25610.1	ATRD22, RD22	BURP domain-containing protein
0	MDC027439.4: 1106-2173	1.79769e+308			
0	MDC027586.25: 17627-18649	3.74147	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
0	MDC027586.25: 9596-10534	3.70806	AT3G54200.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDP0000229796	MDC028034.30: 3913-5269	1.79769e+308	AT4G10490.1		2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein
MDP0000317816	MDC029025.16: 37724-39632	-2.22916	AT5G01600.1	ATFER1, FER1	ferretin 1
MDP0000227827	MDC029110.8: 34469-35629	-2.14091	AT2G03550.1		alpha/beta-Hydrolases superfamily protein
MDP0000246508	MDC029331.22: 370-647	1.85922			
MDP0000228456	MDC029335.25: 6007-7048	2.82399	AT2G15760.1		Protein of unknown function (DUF1645)
0	MDC029401.43: 2619-2642	1.79769e+308			
0	MDC029428.27: 19524-19555	1.79769e+308			
MDP0000357899	MDC029522.47: 22578-23050	1.79769e+308			
MDP0000390563	MDC029522.47: 26456-26678	1.79769e+308			
0	MDC029522.47: 29375-29799	1.79769e+308			
MDP0000228257	MDC029541.17: 30026-31667	-2.98044	AT5G15240.1		Transmembrane amino acid transporter family protein
MDP0000782085	MDC029683.23: 9115-9368	4.22898	AT3G04720.1	HEL, PR-4, PR4	pathogenesis-related 4
0	MDC029690.2: 317-603	1.79769e+308			
0	MDC031150.12: 8267-8723	1.79769e+308	AT4G18160.1	KCO6, ATTPK3, ATKCO6, TPK3	Ca2+ activated outward rectifying K+ channel 6
MDP0000910895	MDC031261.10: 30690-31071	1.79769e+308	AT5G11970.1		Protein of unknown function (DUF3511)
MDP0000316468	MDC032201.3: 1004-1193	1.79769e+308			
MDP0000227463	MDC032660.9: 5945-14498	6.5024	AT2G21440.1		RNA-binding (RRM/RBD/RNP motifs) family protein
MDP0000705797	MDC034940.5: 2269-7814	-2.70526	AT4G30430.1	TET9	tetraspanin9
MDP0000595200	MDC035405.21: 18653-18905	1.79769e+308	AT1G17810.1	BETA-TIP	beta-tonoplast intrinsic protein
MDP0000661371	MDC035507.15: 17028-17370	-2.3258	AT5G59320.1	LTP3	lipid transfer protein 3

MDP0000228304	MDC035519.7: 9734-13224	4.85453	AT3G56400.1	ATWRKY70, WRKY70	WRKY DNA-binding protein 70
MDP0000761113	MDC035533.8: 11708-13073	2.77336	AT2G14095.1		
MDP0000143463	MDC035751.16: 12042-12657	4.53253	AT4G37290.1		
MDP0000143462	MDC035751.16: 9288-9911	4.88732	AT4G37290.1		
0	MDC036102.13: 6186-6377	1.79769e+308			
0	MDC036190.10: 2148-2600	4.37825			
MDP0000859897	MDC037018.11: 5057-5594	1.79769e+308	AT2G45760.1	BAL, BAP2	BON association protein 2
MDP0000478473	MDC037119.7: 1598-3986	1.97805	AT5G36110.1	CYP716A1	cytochrome P450, family 716, subfamily A, polypeptide 1
0	MDC037361.9: 6784-7143	1.79769e+308			
MDP0000836051	MDC037826.18: 47629-48283	3.29594	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
0	MDC038019.6: 878-1176	1.79769e+308			
MDP0000739955	MDC038611.7: 8913-9138	4.66013			
MDP0000739957	MDC038611.7: 9423-17275	1.79769e+308			
MDP0000229364	MDC039821.7: 261-870	3.78343	AT1G24020.1	MLP423	MLP-like protein 423
0	MDC039927.8: 6532-7016	1.79769e+308	AT5G45230.1		Disease resistance protein (TIR-NBS-LRR class) family
MDP0000317158	MDC039977.12: 10248-22411	-1.92458	AT2G42990.1		GDSL-like Lipase/Acylhydrolase superfamily protein
MDP0000627178	MDC039977.12: 10248-22411	2.53116	AT3G11660.1	NHL1	NDR1/HIN1-like 1
MDP0000246775	MDC040311.10: 4864-6142	1.95053	AT1G75800.1		Pathogenesis-related thaumatin superfamily protein
MDP0000635659	MDC041102.8: 8881-9496	2.0994	AT1G17860.1		Kunitz family trypsin and protease inhibitor protein
MDP0000134064	MDC042250.3: 3997-5643	1.79769e+308			
MDP0000345608	MDC043994.10: 1318-1504	1.79769e+308			

Table 4 Annotation of previously unassigned significantly differential expressed *M. x domestica* transcripts in response to *E*. a*mylovora* two days post inoculation. A BLASTX analysis was performed using the *A*. *thaliana* TAIR 10 database as reference.

M. x domestica loci	*A. thaliana* accession	Name	Description
MDC000127.652: 4251-4492	AT4G33720.1		CAP (Cysteine-rich secretory proteins, Antigen 5, and Pathogenesis-related 1 protein) superfamily protein
MDC000446.497: 2613-3451	AT3G19615.1		unknown protein
MDC000455.144: 3026-3468	AT4G24620.1	PGI1, PGI	phosphoglucose isomerase 1
MDC001441.272: 13692-14163	AT5G43920.1		transducin family protein / WD-40 repeat family protein
MDC001471.424: 93507-93619	AT2G29260.1		NAD(P)-binding Rossmann-fold superfamily protein
MDC001671.165: 2805-2973	AT1G78380.1	ATGSTU19, GST8, GSTU19	glutathione S-transferase TAU 19
MDC001963.417: 4816-4925	AT4G27250.2		NAD(P)-binding Rossmann-fold superfamily protein
MDC002322.251: 26803-27928	AT4G11280.1	ACS6, ATACS6	1-aminocyclopropane-1-carboxylic acid (acc) synthase 6
MDC002431.300: 11772-11965	AT5G19130.2		GPI transamidase component family protein / Gaa1-like family protein

MDC002799.293: 2023-2423	AT2G29330.1	TRI	tropinone reductase
MDC003306.225: 3010-3406	AT2G16850.1	PIP3B, PIP2;8	plasma membrane intrinsic protein 2;8
MDC003716.306: 46958-47066	AT1G03260.1		SNARE associated Golgi protein family
MDC004097.232: 8798-9675	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC004475.200: 15597-16341	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC005490.240: 8153-8416	AT5G66180.3		S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
MDC005927.393: 5902-6584	AT5G10830.1		S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
MDC006260.462: 8079-8672	AT1G23440.1		Peptidase C15, pyroglutamyl peptidase I-like
MDC006289.408: 7320-7584	AT2G45960.3	PIP1B, TMP-A, ATHH2, PIP1;2	plasma membrane intrinsic protein 1B
MDC006603.734: 2300-2410	AT5G39110.1		RmlC-like cupins superfamily protein
MDC007088.513: 4786-5156	AT5G24810.2		ABC1 family protein
MDC007581.595: 2473-2576	AT4G28460.1		unknown protein
MDC007779.587: 2989-3343	AT3G14630.1	CYP72A14	cytochrome P450, family 72, subfamily A, polypeptide 14
MDC007779.587: 3489-4308	AT3G14680.1	CYP72A9	cytochrome P450, family 72, subfamily A, polypeptide 9
MDC008017.329: 6473-7175	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC008031.166: 8984-9384	AT3G60030.1	SPL12	squamosa promoter-binding protein-like 12
MDC008212.493: 3616-4058	AT5G43180.1		Protein of unknown function, DUF599
MDC008216.318: 26921-27156	AT4G20820.1		FAD-binding Berberine family protein
MDC008563.271: 10114-10663	AT1G75620.1		glyoxal oxidase-related protein
MDC009139.374: 7848-8934	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC009630.367: 24050-24262	AT2G03810.4		18S pre-ribosomal assembly protein gar2-related
MDC009830.388: 3008-4348	AT5G13930.1	CHS, TT4, ATCHS	Chalcone and stilbene synthase family protein
MDC010174.397: 1163-1411	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC010474.340: 3456-4185	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC010476.238: 18498-19659	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC010912.583: 5714-6300	AT2G36380.1	PDR6, ATPDR6	pleiotropic drug resistance 6
MDC010981.245: 18382-19274	AT3G61510.1	ACS1, AT-ACS1	ACC synthase 1
MDC011449.97: 11886-12570	AT2G18680.1		unknown protein
MDC011459.391: 12253-12872	AT2G39210.1		Major facilitator superfamily protein
MDC011603.242: 16362-17137	AT4G33720.1		CAP (Cysteine-rich secretory proteins, Antigen 5, and Pathogenesis-related 1 protein) superfamily protein
MDC011770.416: 7739-8412	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family

MDC011773.84: 2484-3065	AT2G23270.1		unknown protein
MDC012392.481: 2083-2367	AT2G29420.1	ATGSTU7, GST25, GSTU7	glutathione S-transferase tau 7
MDC012392.481: 2550-3061	AT3G09270.1	ATGSTU8, GSTU8	Glutathione S-transferase TAU 8
MDC012733.121: 11561-12529	AT4G11280.1	ACS6, ATACS6	1-aminocyclopropane-1-carboxylic acid (acc) synthase 6
MDC012900.215: 12407-12925	AT5G01710.1		methyltransferases
MDC013340.296: 1896-2851	AT5G66900.1		Disease resistance protein (CC-NBS-LRR class) family
MDC013531.194: 13169-13505	AT3G54820.1	PIP2D, PIP2;5	plasma membrane intrinsic protein 2;5
MDC013883.433: 28953-29243	AT2G27450.2	NLP1, ATNLP1, CPA	nitrilase-like protein 1
MDC015077.305: 4104-4809	AT2G45570.1	CYP76C2	cytochrome P450, family 76, subfamily C, polypeptide 2
MDC015146.108: 31720-32772	AT2G04780.2	FLA7	FASCICLIN-like arabinoogalactan 7
MDC015272.259: 4201-4401	AT3G02050.1	KUP3, ATKUP3, ATKT4	K+ uptake transporter 3
MDC015771.323: 788-1107	AT1G31910.1		GHMP kinase family protein
MDC016234.268: 19756-19922	AT5G07050.1		nodulin MtN21 /EamA-like transporter family protein
MDC017013.566: 1815-2228	AT2G45220.1		Plant invertase/pectin methylesterase inhibitor superfamily
MDC017013.566: 2346-2726	AT2G45220.1		Plant invertase/pectin methylesterase inhibitor superfamily
MDC017013.566: 514-1355	AT2G45220.1		Plant invertase/pectin methylesterase inhibitor superfamily
MDC017130.237: 1246-1897	AT1G18390.2		Protein kinase superfamily protein
MDC017450.136: 8789-9313	AT3G16340.2	PDR1	pleiotropic drug resistance 1
MDC017540.252: 44737-45439	AT4G20820.1		FAD-binding Berberine family protein
MDC017935.299: 4662-5932	AT1G30700.1		FAD-binding Berberine family protein
MDC018101.293: 13762-13915	AT1G10010.1	AAP8, ATAAP8	amino acid permease 8
MDC018495.75: 656-1593	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC018532.136: 875-1203	AT4G25340.2	FKBP53	FK506 BINDING PROTEIN 53
MDC018858.178: 25373-25918	AT1G01490.2		Heavy metal transport/detoxification superfamily protein
MDC019060.82: 24775-25363	AT1G01490.2		Heavy metal transport/detoxification superfamily protein
MDC019105.344: 1605-2183	AT4G23160.1	CRK8	cysteine-rich RLK (RECEPTOR-like protein kinase) 8
MDC019583.195: 2352-2815	AT2G37760.1		NAD(P)-linked oxidoreductase superfamily protein
MDC019583.195: 3051-3246	AT2G37770.2		NAD(P)-linked oxidoreductase superfamily protein
MDC020082.224: 15608-15824	AT1G66950.1	PDR11, ATPDR11	pleiotropic drug resistance 11
MDC020082.224: 16228-16490	AT2G36380.1	PDR6, ATPDR6	pleiotropic drug resistance 6
MDC020082.224: 16703-17360	AT2G36380.1	PDR6, ATPDR6	pleiotropic drug resistance 6

MDC020098.119: 12808-13292	AT3G16340.2	PDR1	pleiotropic drug resistance 1
MDC020206.60: 80379-80919	AT3G48180.1		unknown protein
MDC021555.260: 3534-3862	AT4G20970.1		basic helix-loop-helix (bHLH) DNA-binding superfamily protein
MDC021563.286: 640-1084	AT5G37850.3	SOS4	pfkB-like carbohydrate kinase family protein
MDC021658.157: 9449-9957	AT1G60950.1	FED A, ATFD2	2Fe-2S ferredoxin-like superfamily protein
MDC022115.179: 2130-2784	AT5G06320.1	NHL3	NDR1/HIN1-like 3
MDC022366.63: 24207-24828	AT5G13220.4		jasmonate-zim-domain protein 10
MDC022531.114: 4018-4893	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC022879.56: 1375-1884	AT2G22420.1		Peroxidase superfamily protein
MDC027586.25: 17627-18649	AT2G46150.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC027586.25: 9596-10534	AT3G54200.1		Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family
MDC031150.12: 8267-8723	AT4G18160.1	KCO6, ATTPK3, ATKCO6, TPK3	Ca2+ activated outward rectifying K+ channel 6
MDC039927.8: 6532-7016	AT5G45230.1		Disease resistance protein (TIR-NBS-LRR class) family

Table 5 Annotation of previously unassigned expressed *M. x domestica* transcripts two days post inoculation. A BLASTX analysis was performed using the *A. thaliana* TAIR 10 database as reference.

M. x domestica locus	*A. thaliana* accession	PFAM	Panther	Clusters of orthologous groups	Enzyme code	KEGG orthology	Description
MDC000047.154: 15534-16428	AT5G10840.1	PF02990	PTHR10766	KOG1278			transmembrane 9 superfamily member, putative
MDC001087.439: 6147-6450	AT5G20790.2						
MDC011504.316: 3604-3768	AT5G56670.1	PF04758	PTHR12650	KOG0009		K02983	expressed protein
MDC011558.545: 2913-3398	AT4G38840.1	PF02519				K14488	OsSAUR31 - Auxin-responsive SAUR gene family member
MDC011558.545: 10592-11117	AT4G38840.1	PF02519				K14488	OsSAUR31 - Auxin-responsive SAUR gene family member
MDC011670.126: 374-634	AT2G44620.1	PF00550	PTHR20863	KOG1748	1.6.5.3, 1.6.99.3	K03955	acyl carrier protein, putative
MDC011700.243: 1227-1605	AT5G08139.1	PF00097	PTHR22763	KOG1493			zinc finger, C3HC4 type domain containing protein
MDC011702.243: 1833-2070	AT2G37660.1		PTHR14194	KOG1203			NAD dependent epimerase/dehydratase family protein, putative
MDC011702.243: 3359-3717	AT2G37660.1		PTHR14194	KOG1203			NAD dependent epimerase/dehydratase family protein, putative
MDC011704.133: 1724-2278	AT5G20680.3	PF03005					expressed protein
MDC011727.163: 5647-5848	AT3G04730.1	PF02309					OsIAA30 - Auxin-responsive Aux/IAA gene family member
MDC011727.163: 7232-7693	AT3G04730.1	PF02309					OsIAA30 - Auxin-responsive Aux/IAA gene family member
MDC011766.689: 5483-5959	AT2G20142.1	PF01582					expressed protein

MDC011768.383: 32501-33098	AT3G23920.1	PF01373					beta-amylase, putative
MDC011804.393: 6327-6784	AT3G51670.1	PF03765, PF00650	PTHR23324	KOG1471			patellin protein, putative
MDC011809.297: 12013-12383	AT3G44280.1						expressed protein
MDC011970.92: 16025-16891	AT3G13920.4	PF00270, PF00271	PTHR10967	KOG0328			DEAD-box ATP-dependent RNA helicase, putative
MDC011970.92: 17409-17837	AT1G54270.2	PF00270, PF00271	PTHR10967	KOG0327		K03257	DEAD-box ATP-dependent RNA helicase, putative
MDC012057.108: 18172-18502	AT1G11170.1	PF05212					lysine ketoglutarate reductase trans-splicing related 1, putative
MDC012065.78: 5672-5927	AT1G79040.1	PF04725				K03541	photosystem II 10 kDa polypeptide, putative
MDC012139.232: 7565-8258	AT1G73100.1	PF02182, PF05033, PF00856	PTHR22884	KOG1082			histone-lysine N-methyltransferase, H3 lysine-9 specific SUVH1, putative
MDC001187.272: 8633-8985	AT1G36050.2	PF07970	PTHR10984	KOG2667			endoplasmic reticulum-Golgi intermediate compartment protein 3, putative
MDC012149.217: 8136-8679	AT1G48830.2	PF01251	PTHR11278	KOG3320			40S ribosomal protein S7, putative
MDC012246.289: 9924-10344	AT2G30710.1	PF00566	PTHR22957	KOG1092			TBC domain containing protein
MDC012278.208: 17918-18313	AT5G62790.2	PF02670, PF08436			1.1.1.267	K00099	1-deoxy-D-xylulose 5-phosphate reductoisomerase, putative
MDC012291.307: 22481-23638	AT2G16365.4	PF00646					expressed protein
MDC012304.216: 7950-8423	AT1G05660.1	PF00295					polygalacturonase, putative
MDC012304.216: 8670-9266	AT1G02790.1	PF00295			3.2.1.67	K01213	polygalacturonase, putative
MDC012329.239: 6033-6692	AT5G05340.1	PF00141			1.11.1.7	K00430	peroxidase precursor, putative
MDC001207.483: 41049-41732	AT1G16560.4	PF04080	PTHR13148				per1-like family protein, putative
MDC012329.239: 7209-7460	AT5G58390.1	PF00141			1.11.1.7	K00430	peroxidase precursor, putative
MDC012329.239: 7574-7771	AT5G58390.1	PF00141			1.11.1.7	K00430	peroxidase precursor, putative
MDC012329.239: 8539-8816	AT5G05340.1	PF00141			1.11.1.7	K00430	peroxidase precursor, putative
MDC012329.239: 18042-18170	AT2G30330.1	PF06320	PTHR13073	KOG3390			expressed protein
MDC012329.239: 18286-18476	AT2G30330.1	PF06320	PTHR13073	KOG3390			expressed protein
MDC012392.517: 8036-8280	AT1G78380.1	PF02798, PF00043	PTHR11260	KOG0406			glutathione S-transferase, putative
MDC012438.121: 1208-1390	AT4G29260.1	PF03767					HAD superfamily phosphatase, putative
MDC012447.123: 2145-2841	AT4G01370.1	PF00069	PTHR11295	KOG0660	2.7.11.24	K04371	CGMC_MAPKCMGC_2_ERK.14 - CGMC includes CDA, MAPK, GSK3, and CLKC kinases
MDC012491.393: 4-602	AT3G14840.2	PF00560, PF11721, PF07714, PF00069	PTHR23258	KOG1187			receptor-like protein kinase 2, putative
MDC012491.394: 7041-7535	AT3G14840.2	PF00560, PF11721, PF07714, PF00069	PTHR23258	KOG1187			receptor-like protein kinase 2, putative
MDC012594.475: 10716-11062	AT4G04630.1	PF04520					DUF584 domain containing protein, putative
MDC012645.61: 1423-1710	AT1G56700.2		PTHR23402	KOG4755			pyrrolidone-carboxylate peptidase, putative
MDC012725.448: 862-977	AT5G11260.1	PF00170, PF07716	PTHR13301				bZIP transcription factor domain containing protein
MDC012817.629: 817-1307	AT2G38000.1	PF00684		KOG2813			expressed protein
MDC012823.282: 222-434	AT3G15690.2	PF00364	PTHR18866:SF1				

MDC012824.191: 6532-7133	AT1G30330.2	PF02362, PF06507, PF02309					auxin response factor, putative
MDC012868.151: 2447-3068	AT1G79200.1		PTHR18460				splicing factor, arginine/serine-rich 12, putative
MDC012916.334: 10310-10713	AT3G21700.2	PF08477	PTHR11708	KOG1673			ras-related protein, putative
MDC012916.334: 12813-13262	AT3G21700.1	PF08477	PTHR11708	KOG1673			ras-related protein, putative
MDC012916.334: 13398-13687	AT1G05205.1						expressed protein
MDC012939.284: 5004-5485	AT3G27090.1	PF10539	PTHR23230				N-rich protein, putative
MDC013003.189: 32585-33033	AT3G49590.3	PF10033		KOG4573			expressed protein
MDC013090.275: 11344-11505	AT3G57450.1						conserved hypothetical protein
MDC013096.127: 33850-34454	AT1G15080.1	PF01569	PTHR10165	KOG3030			lipid phosphatase protein, putative
MDC013173.321: 5324-5406	AT5G59840.1	PF00071, PF08477	PTHR11708	KOG0078		K07901	ras-related protein, putative
MDC013184.220: 3935-4234	AT5G47030.1	PF02823	PTHR13822	KOG1758	3.6.3.14	K02134	ATP synthase delta chain, mitochondrial precursor, putative
MDC013211.128: 15219-15773	AT5G12340.1						expressed protein
MDC001250.283: 31328-31743	AT3G06740.1	PF00320	PTHR22949:SF3				expressed protein
MDC013254.184: 26548-26887	AT5G28750.1	PF02416				K03116	mttA/Hcf106 family protein, putative
MDC013272.255: 2408-2881	AT1G24440.1	PF00097		KOG1039			zinc finger, RING-type, putative
MDC013292.269: 3429-3656	AT3G52930.1	PF00274	PTHR11627	KOG1557	4.1.2.13	K01623	fructose-bisphospate aldolase isozyme, putative
MDC001262.252: 30916-31314	AT4G13780.1	PF09334, PF01588	PTHR11946	KOG1247	6.1.1.10	K01874	methionyl-tRNA synthetase, putative
MDC013317.553: 7451-7667	AT2G36630.1	PF01925	PTHR14255				membrane protein, putative
MDC013317.563: 24791-24933	AT5G56670.1	PF04758	PTHR12650	KOG0009		K02983	expressed protein
MDC013338.153: 2636-3071	AT1G18720.1	PF06127		KOG3292			YGL010w, putative
MDC013392.463: 8-454	AT4G31130.1	PF06749					expressed protein
MDC001273.352: 1230-1510	AT1G02680.1	PF02269	PTHR11380	KOG3901		K03127	transcription initiation factor IID, 18kD subunit family protein
MDC013426.256: 1484-1797	AT1G33055.1						expressed protein
MDC013531.194: 10446-10802	AT3G54820.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC013531.194: 10944-11090	AT2G45960.3	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC013531.194: 14302-14625	AT3G53420.2	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC013567.369: 4887-5108	AT5G10700.1		PTHR11717	KOG3305			tyrosine phosphatase, putative
MDC013616.148: 3703-3832	AT5G19140.2	PF12481, PF12504	PTHR11772				stem-specific protein TSJT1, putative
MDC013616.148: 3970-4115	AT5G19140.1	PF12481, PF12504	PTHR11772				stem-specific protein TSJT1, putative
MDC013616.148: 4213-4461	AT5G19140.2	PF12481, PF12504	PTHR11772				stem-specific protein TSJT1, putative
MDC013737.149: 3896-4181	AT4G19645.2	PF03798	PTHR13439	KOG4561			transmembrane protein 56, putative
MDC001279.248: 5742-6162	AT5G16010.1	PF02544	PTHR10556	KOG1638			3-oxo-5-alpha-steroid 4-dehydrogenase, putative
MDC013772.153: 30323-30615	AT3G51100.3						expressed protein
MDC013796.456: 5519-6034	AT3G22930.1	PF00036	PTHR23050	KOG0027		K13448	OsCam2 - Calmodulin

MDC013875.240: 1656-1897	AT5G58240.1	PF01230	PTHR23089	KOG3379	3.6.1.29	K01522	histidine triad family protein, putative
MDC013883.433: 41972-42740	AT2G27730.1						expressed protein
MDC013917.369: 27861-28177	AT5G59970.1	PF00125	PTHR10484	KOG3467		K11254	Core histone H2A/H2B/H3/H4 domain containing protein, putative
MDC013978.597: 11403-11729	AT5G03810.1	PF00657	PTHR22835:SF27				GDSL-like lipase/acylhydrolase, putative
MDC013998.456: 5517-5937	AT3G03000.1	PF00036	PTHR10891	KOG0027		K13448	OsCML11 - Calmodulin-related calcium sensor protein
MDC014084.122: 12618-13135	AT3G04630.3	PF06886					seed specific protein Bn15D14A, putative
MDC014084.127: 14385-14849	AT3G04630.3	PF06886					seed specific protein Bn15D14A, putative
MDC014088.189: 7845-8126	AT3G21770.1	PF00141			1.11.1.7	K00430	peroxidase precursor, putative
MDC014115.478: 5475-5892	AT3G21000.1		PTHR11439				
MDC000185.278: 3219-3514	AT3G62880.2	PF02466					
MDC001325.99: 2744-3063	AT1G11200.1	PF03619	PTHR23423	KOG2641			domain of unknown function domain containing protein
MDC014140.253: 47-409	AT3G47640.3	PF00010					helix-loop-helix DNA-binding domain containing protein
MDC014231.203: 16823-17997	AT2G36460.1	PF00274	PTHR11627	KOG1557	4.1.2.13	K01623	fructose-bisphospate aldolase isozyme, putative
MDC015077.305: 3146-3873	AT1G33730.1	PF00067	PTHR19383	KOG0156			cytochrome P450, putative
MDC015153.220: 20005-20108	AT5G54580.1	PF00076	PTHR15241	KOG0114			RNA recognition motif containing protein, putative
MDC015183.122: 8990-9049	AT5G47200.1	PF00071, PF08477	PTHR11708	KOG0084		K07976	ras-related protein, putative
MDC015226.470: 54-427	AT5G36880.2	PF11930, PF00501	PTHR11968	KOG1175	6.2.1.1	K01895	AMP-binding enzyme, putative
MDC015226.508: 6534-6780	AT2G18460.1	PF04367					protein of unknown function DUF502 domain containing protein
MDC015229.223: 18448-18603	AT1G08830.2	PF00080	PTHR10003	KOG0441	1.15.1.1	K04565	copper/zinc superoxide dismutase, putative
MDC015291.262: 409-673	AT4G18040.1	PF01652	PTHR11960	KOG1670		K03259	eukaryotic translation initiation factor, putative
MDC015300.124: 5141-5526	AT4G00026.1	PF08294	PTHR13032	KOG4836			AGAP008572-PA, putative
MDC015306.223: 5385-5889	AT1G25230.1	PF00149	PTHR10161	KOG2679			Ser/Thr protein phosphatase family protein, putative
MDC015317.38: 1691-2088	AT2G19450.1	PF03062	PTHR10408	KOG0380	2.3.1.20, 2.3.1.75, 2.3.1.76	K11155	O-acyltransferase, putative
MDC015354.268: 3980-4636	AT2G45260.1	PF04859					GIL1, putative
MDC015354.268: 26756-27169	AT2G45240.1	PF01753, PF00557	PTHR10804	KOG2738	3.4.11.18	K01265	peptidase, M24 family protein, putative
MDC015354.268: 30817-30986	AT2G45240.1	PF01753, PF00557	PTHR10804	KOG2738	3.4.11.18	K01265	peptidase, M24 family protein, putative
MDC015361.139: 5122-6154	AT1G53910.3	PF00847				K09286	AP2 domain containing protein
MDC015361.232: 11883-12412	AT4G17050.1	PF07883					cupin 2, conserved barrel domain protein, putative
MDC015377.320: 8056-8386	AT1G16250.1	PF00646, PF07646, PF01344	PTHR23230				OsFBK22 - F-box domain and kelch repeat containing protein
MDC015388.349: 245-728	AT2G33590.1	PF01370	PTHR10366	KOG1502			reductase, putative
MDC001370.310: 10351-10720	ATMG00300.1		PTHR11439				
MDC015405.307: 5999-6733	AT2G27730.1						expressed protein
MDC015405.307: 11611-12008	AT2G27450.2	PF00795	PTHR23088	KOG0806			N-carbamoylputrescine amidase, putative

MDC015460.735: 786-1170	AT3G17020.1	PF00582					universal stress protein domain containing protein, putative
MDC015489.206: 24262-35335	AT4G12080.1	PF03479					AT hook motif domain containing protein
MDC015491.125: 1309-1363	AT4G31300.3	PF00227	PTHR11599	KOG0174	3.4.25.1	K02738	peptidase, T1 family, putative
MDC015509.61: 2649-2790	AT5G63160.1	PF00651, PF02135	PTHR23230	KOG1778			BTBZ2 - Bric-a-Brac, Tramtrack, and Broad Complex BTB domain with TAZ zinc finger and Calmodulin-binding domains
MDC015520.222: 32010-33690	AT5G10770.1		PTHR13683	KOG1339			aspartic proteinase nepenthesin-2 precursor, putative
MDC015556.295: 6786-7196	AT4G00030.1	PF04755					PAP fibrillin family domain containing protein
MDC015585.34: 19739-20189	AT3G54280.2	PF02985, PF12054, PF00176, PF00271	PTHR10799	KOG0392			SNF2 family N-terminal domain containing protein
MDC015655.486: 8519-9001	AT5G62200.1	PF06232					embryo-specific 3, putative
MDC015715.117: 4672-5113	AT4G16580.1		PTHR12320	KOG1379			stage II sporulation protein E, putative
MDC015785.318: 410-690	AT3G16080.1	PF01907	PTHR10768	KOG3475		K02922	ribosomal protein L37, putative
MDC015861.221: 33780-34101	AT2G16430.2	PF00149	PTHR22953	KOG1378			purple acid phosphatase precursor, putative
MDC015884.83: 20968-21098	AT1G50370.1	PF00149	PTHR11668	KOG0373	3.1.3.16	K01090	Ser/Thr protein phosphatase family protein, putative
MDC015884.83: 23952-24093	AT3G19980.1	PF00149	PTHR11668	KOG0373	3.1.3.16	K01090	Ser/Thr protein phosphatase family protein, putative
MDC015884.83: 25428-25873	AT3G19980.1	PF00149	PTHR11668	KOG0373	3.1.3.16	K01090	Ser/Thr protein phosphatase family protein, putative
MDC015885.118: 3197-3618	AT1G15520.1	PF00005, PF01061, PF08370	PTHR19241	KOG0065			pleiotropic drug resistance protein, putative
MDC015885.118: 3742-3985	AT1G15520.1	PF00005, PF01061, PF08370	PTHR19241	KOG0065			pleiotropic drug resistance protein, putative
MDC001441.272: 2572-3023	AT3G04300.1	PF05899					enzyme of the cupin superfamily protein, putative
MDC015915.252: 7548-9246	AT5G02500.1	PF00012	PTHR19375	KOG0100		K03283	DnaK family protein, putative
MDC016026.76: 14360-14736	AT1G30580.1	PF01926, PF06071	PTHR23305	KOG1491		K06942	GTP-binding protein, putative
MDC016027.22: 3681-3837	AT4G21105.1	PF02238					COX VIIa, putative
MDC016044.175: 22582-23026	ATMG00310.1		PTHR19446				conserved hypothetical protein
MDC001441.272: 13137-13500	AT5G43920.1	PF00400	PTHR22838	KOG0293			WD repeat-containing protein, putative
MDC016050.65: 24-224	AT3G51000.1	PF12146, PF00561	PTHR10992	KOG4178			hydrolase, alpha/beta fold family domain containing protein
MDC016095.141: 7510-7595	AT5G59840.1	PF00071, PF08477	PTHR11708	KOG0078		K07901	ras-related protein, putative
MDC016096.158: 472-890	AT4G21490.1	PF07992, PF00070, PF00036	PTHR22915	KOG2495	1.6.99.3	K03885	NADH-ubiquinone oxidoreductase, mitochondrial precursor, putative
MDC016098.147: 4891-5339	AT1G55280.1	PF03899					expressed protein
MDC000193.346: 9537-9769	AT3G04400.2	PF00238	PTHR11761	KOG0901		K02894	ribosomal protein, putative
MDC016152.155: 52339-52623	AT5G27760.1	PF04588					hypoxia-responsive family protein, putative
MDC016186.171: 1006-1298	AT3G58970.1		PTHR13890	KOG2662			CorA-like magnesium transporter protein, putative
MDC016186.171: 1596-2066	AT3G51890.1		PTHR10639				expressed protein
MDC001471.424: 94139-94333	AT2G29170.1		PTHR19410				oxidoreductase, short chain dehydrogenase/reductase family domain containing protein
MDC016234.268: 19514-19639	AT5G07050.1	PF00892					auxin-induced protein 5NG4, putative

MDC016234.268: 20057-20273	AT5G07050.1	PF00892					auxin-induced protein 5NG4, putative
MDC016234.268: 20680-20980	AT5G07050.1	PF00892					auxin-induced protein 5NG4, putative
MDC016261.58: 2022-2456	AT4G21460.1	PF10213	PTHR13490:SF4				expressed protein
MDC016265.275: 3809-5168	AT4G21990.1	PF01507, PF00085	PTHR18929	KOG0189	1.8.4.9	K05907	
MDC016279.371: 5166-5698	AT4G16360.3	PF04739	PTHR10343	KOG1616			SNF1-related protein kinase regulatory subunit beta-1, putative
MDC016282.141: 417-597	AT4G22220.1	PF01592	PTHR10093	KOG3361			iron-sulfur cluster assembly enzyme ISCU, mitochondrial precursor, putative
MDC016368.213: 31185-31562	AT5G24350.2	PF08314		KOG1797			expressed protein
MDC001530.209: 10977-11259	AT3G61040.1	PF00067	PTHR19383	KOG0156			cytochrome P450, putative
MDC016613.108: 4593-5046	AT2G33590.1	PF01370	PTHR10366	KOG1502			reductase, putative
MDC016680.236: 5904-6226	AT4G38790.1	PF00810	PTHR10585	KOG3106			ER lumen protein retaining receptor, putative
MDC001542.287: 23512-23825	AT3G30340.1	PF00892					auxin-induced protein 5NG4, putative
MDC016719.244: 7540-8369	AT5G41330.1	PF02214	PTHR11145	KOG2714			B4-BTB4 - Bric-a-Brac, Tramtrack, Broad Complex BTB domain with B4 subfamily conserved sequence
MDC016733.266: 3079-3967	AT5G56670.1	PF04758	PTHR12650	KOG0009		K02983	expressed protein
MDC016767.549: 526-899	AT1G21630.2	PF00036	PTHR11216	KOG0998			EF hand family protein, putative
MDC016767.586: 2807-3215	AT1G21630.1	PF00036	PTHR11216	KOG0998			EF hand family protein, putative
MDC016797.262: 982-1299	AT2G24860.1						tsi1-interacting protein TSIP1, putative
MDC001544.220: 3084-3414	AT3G50440.1	PF00561	PTHR10992	KOG1454			OsPOP4 - Putative Prolyl Oligopeptidase homologue
MDC016994.91: 1058-1430	AT5G58740.1	PF04969	PTHR12356	KOG2265			CS domain containing protein, putative
MDC001568.219: 2517-2945	AT1G42960.1						expressed protein
MDC017149.109: 416-866	AT3G17020.1	PF00582					universal stress protein domain containing protein, putative
MDC017149.109: 1733-2403	AT3G36659.1	PF04043	PTHR22931:SF5				IWS1 homolog A, putative
MDC017203.93: 49693-51044	AT2G32070.1	PF04857	PTHR10797	KOG0304			CAF1 family ribonuclease containing protein, putative
MDC017207.68: 1532-2126	AT2G01650.1	PF00096, PF09409, PF00789	PTHR23153	KOG2699		K14011	UBX domain containing protein
MDC017303.260: 762-1075	AT1G11880.1	PF04188	PTHR12468	KOG2647	2.4.1.-	K07542	GPI mannosyltransferase 2, putative
MDC017303.263: 3880-4185	AT1G11880.1	PF04188	PTHR12468	KOG2647	2.4.1.-	K07542	GPI mannosyltransferase 2, putative
MDC017342.179: 6762-7645	AT1G04170.1	PF00009, PF03144, PF09173	PTHR23115	KOG0466		K03242	eukaryotic translation initiation factor 2 subunit gamma, putative
MDC001577.2956: 23137-23237	AT3G52930.1	PF00274	PTHR11627	KOG1557	4.1.2.13	K01623	fructose-bisphospate aldolase isozyme, putative
MDC017415.336: 1875-2679	AT3G13275.1						
MDC017440.359: 16037-16253	AT4G29230.1	PF02365					no apical meristem protein, putative
MDC001577.2956: 23551-23754	AT5G03690.2	PF00274	PTHR11627	KOG1557	4.1.2.13	K01623	fructose-bisphospate aldolase isozyme, putative
MDC017491.272: 6014-6252	AT2G37660.1		PTHR14194	KOG1203			NAD dependent epimerase/dehydratase family protein, putative
MDC017491.272: 7509-7862	AT2G37660.1		PTHR14194	KOG1203			NAD dependent epimerase/dehydratase family protein, putative

MDC017518.269: 8615-8848	AT1G05190.1	PF00347	PTHR11655	KOG3254			ribosomal protein L6, putative
MDC017518.269: 9967-10438	AT1G05190.1	PF00347	PTHR11655	KOG3254			ribosomal protein L6, putative
MDC017540.252: 42046-42444	AT4G20840.1	PF01565, PF08031	PTHR11748				reticuline oxidase-like protein precursor, putative
MDC017540.252: 45858-46351	AT5G44410.1	PF01565, PF08031					reticuline oxidase-like protein precursor, putative
MDC017548.358: 6850-7605	AT2G09990.1	PF00380	PTHR21569	KOG1753		K02960	ribosomal protein, putative
MDC017550.46: 15204-15624	AT5G59970.1	PF00125	PTHR10484	KOG3467		K11254	Core histone H2A/H2B/H3/H4 domain containing protein, putative
MDC000205.451: 1016-1345	AT5G43600.1	PF01546, PF07687	PTHR11014				peptidase, putative
MDC001577.2956: 23830-23966	AT3G52930.1	PF00274	PTHR11627	KOG1557	4.1.2.13	K01623	fructose-bisphospate aldolase isozyme, putative
MDC017562.415: 3865-4030	AT5G16400.1	PF00085	PTHR10438	KOG0907			thioredoxin, putative
MDC017562.415: 5319-5607	AT3G02730.1	PF00085	PTHR10438	KOG0907			thioredoxin, putative
MDC017580.217: 171-361	AT5G15780.1	PF01190					POEI17 - Pollen Ole e I allergen and extensin family protein precursor
MDC017593.111: 3812-4134	AT2G44650.1	PF00166	PTHR10772	KOG1641			chaperonin, putative
MDC017611.70: 9398-9922	AT5G16790.1	PF05615	PTHR14854	KOG3215		K13176	THO complex subunit 7, putative
MDC017634.105: 22460-22837	AT1G15000.1	PF00450	PTHR11802	KOG1282	3.4.16.-	K09645	OsSCP31 - Putative Serine Carboxypeptidase homologue
MDC017693.122: 6214-6551	AT5G44380.1	PF01565, PF08031	PTHR11748				berberine and berberine like domain containing protein
MDC017695.289: 3392-3935	AT5G60580.4	PF00097	PTHR23012	KOG1609			zinc finger, C3HC4 type, domain containing protein
MDC017782.228: 7791-8049	AT2G28710.1	PF12171, PF00096	PTHR11389				ZOS1-14 - C2H2 zinc finger protein
MDC017817.273: 3318-3686	AT5G07900.1	PF02536		KOG1267			mTERF domain containing protein
MDC017829.667: 3457-3899	AT3G10250.2	PF09713					plant-specific domain TIGR01589 family protein, putative
MDC001605.331: 9735-10084	AT5G10770.1		PTHR13683	KOG1339			aspartic proteinase nepenthesin-2 precursor, putative
MDC017981.251: 962-1158	AT3G48850.1	PF00153	PTHR11896	KOG0767			phosphate carrier protein, mitochondrial precursor, putative
MDC001627.237: 2537-2717	AT1G07440.2	PF00106	PTHR19410	KOG0725			oxidoreductase, short chain dehydrogenase/reductase family protein, putative
MDC018008.230: 9938-10349	AT2G37840.2		PTHR22982		2.7.11.1	K08269	CAMK_CAMK_like_ULKh_APGy.2 - CAMK includes calcium/calmodulin depedent protein kinases
MDC018009.138: 415-646	AT5G37710.1	PF03893, PF01764	PTHR21493	KOG2088			calmodulin-binding heat-shock protein, putative
MDC018060.144: 425-941	AT2G25700.1	PF03931, PF01466	PTHR11165	KOG1724		K03094	SKP1-like protein 1B, putative
MDC001627.237: 2998-3224	AT2G29350.3	PF00106	PTHR19410	KOG0725			oxidoreductase, short chain dehydrogenase/reductase family protein, putative
MDC018073.537: 1656-1915	AT5G65550.1		PTHR11926	KOG1192			glucosyltransferase, putative
MDC018073.590: 292-852	AT5G65550.1		PTHR11926	KOG1192			glucosyltransferase, putative
MDC018099.109: 12995-13315	AT3G17820.1	PF03951, PF00120	PTHR20852	KOG0683	6.3.1.2	K01915	glutamine synthetase, catalytic domain containing protein
MDC018139.149: 19551-19623	AT4G34700.1	PF05347	PTHR12868	KOG3466	1.6.5.3, 1.6.99.3	K03965	LYR motif containing protein, putative
MDC018160.157: 3495-3833	AT2G16850.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC018160.157: 3922-4062	AT5G60660.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative

MDC001627.237: 4701-5152	AT2G29330.1	PF00106	PTHR19410	KOG0725	1.1.1.206	K08081	oxidoreductase, short chain dehydrogenase/reductase family domain containing protein
MDC018160.157: 4161-4370	AT4G35100.2	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC018160.157: 4570-4823	AT2G16850.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC018334.222: 6621-6929	AT2G46070.2	PF00069, PF07714	PTHR11295	KOG0660	2.7.11.24	K04371	CGMC_MAPKCMGC_2_ERK.13 - CGMC includes CDA, MAPK, GSK3, and CLKC kinases
MDC018355.124: 5469-5749	AT2G32950.1	PF00097, PF00400	PTHR22847	KOG0265	6.3.2.19	K10143	COP1, putative
MDC018359.70: 1069-1579	AT2G02230.1	PF00646					OsFBX70 - F-box domain containing protein
MDC018409.250: 3724-4557	AT2G09990.1	PF00380	PTHR21569	KOG1753		K02960	ribosomal protein, putative
MDC018412.103: 26641-27151	AT3G01360.2	PF04819					viral-response family protein
MDC018491.206: 16889-17230	AT5G11110.1	PF08550, PF00534	PTHR12526	KOG0853			sucrose-phosphate synthase, putative
MDC018507.307: 20436-20547	AT1G23260.1	PF00179	PTHR11621	KOG0896		K10704	ubiquitin-conjugating enzyme, putative
MDC018507.307: 20621-20737	AT2G36060.3		PTHR11621	KOG0896		K10704	ubiquitin-conjugating enzyme, putative
MDC018507.307: 20888-21033	AT1G23260.1	PF00179	PTHR11621	KOG0896		K10704	ubiquitin-conjugating enzyme, putative
MDC018556.272: 150-522	AT5G11760.1	PF08576					expressed protein
MDC001661.298: 30577-31330	AT1G01980.1	PF01565, PF08031		KOG1231			reticuline oxidase-like protein precursor, putative
MDC018580.424: 39-984	AT3G58030.4	PF00097	PTHR12313	KOG0823			zinc finger, C3HC4 type domain containing protein
MDC018648.267: 14763-15015	AT3G44260.1	PF04857	PTHR10797	KOG0304			CAF1 family ribonuclease containing protein, putative
MDC018648.267: 15175-15555	AT3G44260.1	PF04857	PTHR10797	KOG0304			CAF1 family ribonuclease containing protein, putative
MDC018667.247: 1783-1896	AT4G23880.1						
MDC001665.416: 2559-2944	AT4G38020.1	PF00588	PTHR12029	KOG2506			RNA methyltransferase, TrmH family protein, putative
MDC018728.83: 12896-13234	AT3G05545.1	PF00097	PTHR22766				zinc finger, C3HC4 type domain containing protein
MDC018728.83: 23735-24128	AT3G05530.1	PF07728, PF00004	PTHR23073	KOG0652		K03065	26S protease regulatory subunit 6A, putative
MDC018728.83: 24253-24390	AT3G05530.1	PF07728, PF00004	PTHR23073	KOG0652		K03065	26S protease regulatory subunit 6A, putative
MDC018728.83: 24487-24595	AT3G05530.1	PF07728, PF00004	PTHR23073	KOG0652		K03065	26S protease regulatory subunit 6A, putative
MDC018744.264: 10711-11303	AT2G30950.1	PF06480, PF07728, PF00004, PF01434	PTHR23076	KOG0731	3.4.24.-	K03798	OsFtsH2 FtsH protease, homologue of AtFtsH2/8
MDC018744.264: 11400-11646	AT1G06430.1	PF06480, PF07728, PF00004, PF01434	PTHR23076	KOG0731	3.4.24.-	K03798	OsFtsH2 FtsH protease, homologue of AtFtsH2/8
MDC018820.163: 4887-5031	AT1G67530.2	PF04564, PF00514	PTHR22849				armadillo/beta-catenin repeat family protein, putative
MDC018837.177: 26042-26469	AT5G41350.1	PF00097	PTHR22937				zinc finger, C3HC4 type domain containing protein
MDC018870.194: 4803-4978	AT2G33590.1	PF01370	PTHR10366	KOG1502			reductase, putative
MDC018977.108: 28169-28577	AT3G13677.2						expressed protein
MDC018995.224: 13429-13760	AT4G30780.1						expressed protein
MDC019082.128: 8813-9112	AT4G16500.1	PF00031					cysteine proteinase inhibitor 8 precursor, putative
MDC019091.216: 2033-2693	AT5G21940.1						MTD1, putative

MDC019091.231: 35553-36009	AT3G43860.1	PF00759	PTHR22298		3.2.1.4	K01179	endoglucanase, putative
MDC019095.63: 22484-23000	AT5G09590.1	PF00012	PTHR19375	KOG0102		K03283	DnaK family protein, putative
MDC001766.131: 11010-11410	AT4G32760.2	PF00790, PF03127	PTHR13856	KOG1087			VHS and GAT domain containing protein
MDC019117.269: 5681-6073	AT4G13520.1						
MDC019147.46: 9270-9569	AT1G54250.1	PF03870	PTHR10917	KOG3400		K03016	DNA-directed RNA polymerases I, II, and III subunit RPABC3, putative
MDC019238.44: 5191-5727	AT5G18200.1		PTHR11943	KOG2958	2.7.7.12	K00965	galactose-1-phosphate uridyl transferase, putative
MDC019339.84: 8665-9426	AT2G22420.1	PF00141			1.11.1.7	K00430	peroxidase precursor, putative
MDC019360.344: 23048-23730	AT3G59080.2		PTHR13683	KOG1339			aspartic proteinase nepenthesin precursor, putative
MDC019368.126: 5277-5781	AT1G67265.1	PF08137					expressed protein
MDC019383.46: 34094-34336	AT5G48070.1	PF00722, PF06955			2.4.1.207	K08235	glycosyl hydrolases family 16, putative
MDC019400.208: 6391-6498	AT5G47930.1	PF01667	PTHR11594	KOG1779		K02978	40S ribosomal protein S27, putative
MDC019454.54: 10125-10559	AT5G14420.2	PF07002, PF00097	PTHR10857	KOG1327			copine, putative
MDC019461.80: 27261-27542	AT5G52390.1	PF06521					
MDC019461.80: 27755-28178	AT5G52390.1	PF06521					
MDC019484.38: 4830-5300	AT2G39110.1	PF00069, PF07714	PTHR23258	KOG1187			protein kinase APK1A, putative
MDC019522.115: 11000-11388	AT5G11600.1						expressed protein
MDC001859.240: 11026-11424	AT3G55070.1		PTHR12170	KOG0396			macrophage erythroblast attacher, putative
MDC019537.450: 7236-7659	AT3G09700.1		PTHR12763	KOG0723			heat shock protein DnaJ, putative
MDC019598.191: 5158-5543	ATMG00300.1		PTHR11439				
MDC019710.194: 10352-10604	AT1G43650.2	PF00892					integral membrane protein DUF6 containing protein
MDC019710.194: 11838-12171	AT1G43650.1	PF00892					integral membrane protein DUF6 containing protein
MDC019710.194: 13383-13777	AT1G43650.1	PF00892					integral membrane protein DUF6 containing protein
MDC019720.430: 2208-2873	AT5G24860.1						flowering promoting factor-like 1, putative
MDC001883.280: 6135-6504	AT5G16790.1	PF05615	PTHR14854	KOG3215		K13176	THO complex subunit 7, putative
MDC019839.138: 30491-30850	AT4G36130.1	PF00181, PF03947	PTHR13691	KOG2309		K02938	60S ribosomal protein L8, putative
MDC019846.92: 3774-4356	AT5G44380.1	PF01565, PF08031	PTHR11748				berberine and berberine like domain containing protein
MDC019854.101: 11089-11317	AT1G55740.1	PF05691					uncharacterized glycosyltransferase, putative
MDC019950.115: 0-456	AT2G21110.1	PF03018	PTHR21495				dirigent, putative
MDC019959.138: 16420-17121	AT2G44470.3	PF00232	PTHR10353	KOG0626	3.2.1.147	K01237	Os6bglu24 - beta-glucosidase homologue, similar to G. max isohydroxyurate hydrolase
MDC020065.141: 605-1042	AT2G39420.1	PF12146, PF00561	PTHR11614	KOG1455			lipase, putative
MDC020127.174: 13627-13974	AT2G18280.2	PF01167	PTHR16517	KOG2502			OsFBT4 - F-box and tubby domain containing protein
MDC020196.147: 693-1117	AT4G29380.1	PF00069, PF02985, PF00400	PTHR22971	KOG1240	2.7.11.1	K08333	WD domain and HEAT domain containing protein, putative
MDC020226.287: 8976-9718	AT5G46770.1						

MDC020272.72: 5-623	AT3G25600.1	PF00036	PTHR10891	KOG0027		K13448	OsCML14 - Calmodulin-related calcium sensor protein
MDC000218.595: 8811-8927	AT2G18600.1	PF00179	PTHR11621	KOG0420	6.3.2.19	K10579	ubiquitin-conjugating enzyme, putative
MDC020310.146: 2259-2549	AT3G57770.1		PTHR23258				OsWAK53b - OsWAK receptor-like protein kinase
MDC020310.146: 5216-5468	AT3G57770.1		PTHR23258				OsWAK53b - OsWAK receptor-like protein kinase
MDC020353.88: 17968-18166	AT5G66450.2	PF01569	PTHR11247	KOG3146			phosphatase, putative
MDC020364.514: 4946-5132	AT5G15790.2	PF00097	PTHR22766				zinc finger, C3HC4 type domain containing protein
MDC020450.123: 5627-6146	AT4G03030.1	PF00646, PF01344, PF07646	PTHR23230:SF146				OsFBK6 - F-box domain and kelch repeat containing protein
MDC020479.248: 5861-6227	AT1G43640.1	PF00646, PF01167	PTHR16517	KOG2502			OsFBT6 - F-box and tubby domain containing protein
MDC020690.260: 22415-22574	AT5G64200.2	PF00076	PTHR23147	KOG4207		K12891	RNA recognition motif containing protein
MDC020733.167: 1678-2210	AT1G55160.3						expressed protein
MDC020827.218: 21752-22150	AT2G24940.1	PF00173	PTHR10281				cytochrome b5-like Heme/Steroid binding domain containing protein
MDC020867.67: 244-615	AT5G62890.3	PF00860	PTHR11119	KOG1292			nucleobase-ascorbate transporter, putative
MDC021014.157: 18162-18516	AT4G31720.1	PF03540	PTHR21242			K03134	transcription initiation factor TFIID subunit 10, putative
MDC021147.99: 1202-1451	AT2G03500.1	PF00249					MYB family transcription factor, putative
MDC021331.203: 2656-3088	AT5G11650.1	PF12146, PF00561	PTHR11614	KOG1455			hydrolase, alpha/beta fold family domain containing protein
MDC021393.363: 4685-5100	AT4G39730.1	PF01477					wound/stress protein, putative
MDC021461.112: 3144-3560	AT1G79510.2	PF10184		KOG4457			expressed protein
MDC021463.473: 17752-18244	AT4G10840.1	PF07719, PF00515, PF07721	PTHR19959	KOG1840			tetratricopeptide repeat domain containing protein
MDC001963.417: 4488-4646	AT4G27250.2	PF01370	PTHR10366	KOG1502			dihydroflavonol-4-reductase, putative
MDC021607.243: 3134-3692	AT5G10520.1	PF00069, PF07714	PTHR23258	KOG1187			protein kinase domain containing protein
MDC021609.524: 3718-3898	AT5G34850.1	PF00149	PTHR22953	KOG1378			Ser/Thr protein phosphatase family protein, putative
MDC021614.36: 14793-15075	AT1G34760.2	PF00244	PTHR18860	KOG0841			14-3-3 protein, putative
MDC001963.417: 5141-5310	AT4G27250.2	PF01370	PTHR10366	KOG1502			dihydroflavonol-4-reductase, putative
MDC021658.157: 7798-8265	AT1G10950.1	PF02990, PF09680	PTHR10766	KOG1277			transmembrane 9 superfamily member, putative
MDC021663.22: 7322-7560	AT5G59250.1	PF00083, PF07690	PTHR11600	KOG0254			transporter family protein, putative
MDC021673.67: 2187-2416	AT5G15780.1	PF01190					POEI17 - Pollen Ole e I allergen and extensin family protein precursor
MDC021679.163: 8234-8578	AT2G46020.1	PF08880, PF00176, PF00271, PF00439	PTHR10799	KOG0386			SNF2 family N-terminal domain containing protein
MDC021726.381: 2654-2885	AT1G33810.1						expressed protein
MDC021888.183: 8090-8386	AT5G60660.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC021946.181: 5025-5983	AT3G44260.1	PF04857	PTHR10797	KOG0304			CAF1 family ribonuclease containing protein, putative
MDC021991.115: 13313-13634	AT4G34265.2						
MDC022012.425: 3903-4199	AT3G03080.1	PF00107	PTHR11695	KOG1196	1.3.1.74	K08070	NADP-dependent oxidoreductase, putative
MDC002052.246: 116-455	AT3G55360.1	PF02544	PTHR10556	KOG1639	1.3.1.-	K10258	3-oxo-5-alpha-steroid 4-dehydrogenase, putative

MDC022074.29: 9529-10735	AT2G37220.1	PF00076	PTHR10432	KOG0131			RNA recognition motif containing protein, putative
MDC022074.29: 11143-11246	AT2G37220.1	PF00076	PTHR10432	KOG0131			RNA recognition motif containing protein, putative
MDC022078.140: 14217-14720	AT5G64816.2						THION26 - Plant thionin family protein precursor
MDC022085.43: 356-778	AT4G31300.3	PF00227	PTHR11599	KOG0174	3.4.25.1	K02738	peptidase, T1 family, putative
MDC022085.65: 6537-7053	AT4G31300.3	PF00227	PTHR11599	KOG0174	3.4.25.1	K02738	peptidase, T1 family, putative
MDC022086.272: 6317-6499	AT1G07440.2	PF00106	PTHR19410	KOG0725			oxidoreductase, short chain dehydrogenase/reductase family protein, putative
MDC022086.272: 6776-7049	AT1G07440.2	PF00106	PTHR19410	KOG0725			oxidoreductase, short chain dehydrogenase/reductase family protein, putative
MDC022086.272: 7788-8194	AT2G29330.1	PF00106	PTHR19410	KOG0725	1.1.1.206	K08081	oxidoreductase, short chain dehydrogenase/reductase family domain containing protein
MDC022119.74: 4893-5155	AT1G65270.1			KOG4827			expressed protein
MDC022251.179: 6243-7113	AT3G14310.1	PF04043, PF01095					pectinesterase, putative
MDC022362.462: 10497-10811	AT1G03210.1	PF02567	PTHR13774	KOG3033		K06998	phenazine biosynthesis protein, putative
MDC022362.462: 11464-11752	AT4G02860.1	PF02567	PTHR13774	KOG3033			phenazine biosynthesis protein, putative
MDC022376.75: 3053-3379	AT3G03940.1	PF00069	PTHR11909	KOG1164			CK1_CaseinKinase_1a.3 - CK1 includes the casein kinase 1 kinases
MDC022484.73: 18974-19931	AT3G13920.4	PF00270, PF00271	PTHR10967	KOG0328			DEAD-box ATP-dependent RNA helicase, putative
MDC022484.73: 20443-20879	AT1G54270.2	PF00270, PF00271	PTHR10967	KOG0327		K03257	DEAD-box ATP-dependent RNA helicase, putative
MDC002113.246: 13095-13300	AT2G25910.2	PF01612, PF00013	PTHR12124				3-5 exonuclease/ nucleic acid binding protein, putative
MDC022597.70: 2400-2698	AT1G08410.1	PF01926	PTHR11089	KOG1424	3.6.1.-	K14539	GTPase of unknown function domain containing protein, putative
MDC022628.340: 10959-11393	AT2G30950.1	PF06480, PF07728, PF00004, PF01434	PTHR23076	KOG0731	3.4.24.-	K03798	OsFtsH2 FtsH protease, homologue of AtFtsH2/8
MDC022628.340: 12342-12976	AT2G30950.1	PF06480, PF07728, PF00004, PF01434	PTHR23076	KOG0731	3.4.24.-	K03798	OsFtsH2 FtsH protease, homologue of AtFtsH2/8
MDC022628.341: 355-501	AT1G06430.1	PF06480, PF07728, PF00004, PF01434	PTHR23076	KOG0731	3.4.24.-	K03798	OsFtsH2 FtsH protease, homologue of AtFtsH2/8
MDC022637.126: 5119-5368	AT1G19640.1	PF03492			2.1.1.141	K08241	SAM dependent carboxyl methyltransferase, putative
MDC022637.126: 5454-5802	AT1G19640.1	PF03492			2.1.1.141	K08241	SAM dependent carboxyl methyltransferase, putative
MDC022637.126: 6384-6996	AT1G19640.1	PF03492			2.1.1.141	K08241	SAM dependent carboxyl methyltransferase, putative
MDC022638.160: 2961-3442	AT1G13245.1	PF08137					expressed protein
MDC022642.185: 459-976	AT1G45180.1	PF00097	PTHR14155				zinc finger, C3HC4 type domain containing protein
MDC022756.223: 2387-2824	AT2G40935.1	PF04749					uncharacterized Cys-rich domain containing protein, putative
MDC022778.400: 862-1178	AT1G22510.2	PF06803	PTHR22894	KOG4604			zinc finger, C3HC4 type domain containing protein
MDC022787.507: 14430-14765	AT4G23160.1	PF07727, PF01657, PF00069, PF07714, PF11883	PTHR11439	KOG1187			TKL_IRAK_DUF26-lc.20 - DUF26 kinases have homology to DUF26 containing loci
MDC022791.14: 17058-17637	AT5G16970.1	PF00107	PTHR11695	KOG1196	1.3.1.74	K08070	NADP-dependent oxidoreductase, putative
MDC022803.125: 8318-8996	AT5G28540.1	PF00012	PTHR19375	KOG0100		K09490	DnaK family protein, putative
MDC022824.308: 8367-8863	AT4G32551.2	PF08513, PF00400	PTHR22847	KOG0266			transcriptional corepressor LEUNIG, putative

MDC022831.234: 2-828	AT4G17690.1	PF00141			1.11.1.7	K00430	peroxidase family protein
MDC022831.238: 287-403	AT4G27960.2	PF00179	PTHR11621	KOG0417			ubiquitin-conjugating enzyme, putative
MDC022880.59: 13085-13467	AT4G30900.2						endonuclease/exonuclease/phosphatase family protein, putative
MDC022888.364: 12533-12667	AT3G51730.1	PF05184, PF03489	PTHR11480	KOG1340			saposin-like type B, region 1 family protein, putative
MDC022888.364: 12994-13189	AT3G51730.1	PF05184, PF03489	PTHR11480	KOG1340			saposin-like type B, region 1 family protein, putative
MDC022888.364: 14577-14856	AT3G51730.1	PF05184, PF03489	PTHR11480	KOG1340			saposin-like type B, region 1 family protein, putative
MDC023032.62: 43936-44459	AT5G53220.3						expressed protein
MDC023531.44: 2818-2958	AT3G59540.1	PF01781	PTHR10965	KOG3499		K02923	60S ribosomal protein L38, putative
MDC023633.27: 5099-5516	AT3G11670.2				2.4.1.241	K09480	digalactosyldiacylglycerol synthase, putative
MDC023670.41: 2268-2781	AT2G33590.1	PF01370	PTHR10366	KOG1502			reductase, putative
MDC026269.25: 2726-2851	AT5G64730.1	PF00400	PTHR22842	KOG0316		K13124	WD domain, G-beta repeat domain containing protein
MDC026617.62: 10076-10400	AT5G56190.2	PF00400	PTHR22847				WD-40 repeat family protein, putative
MDC002159.340: 12619-13184	AT1G78290.3	PF00069	PTHR22982	KOG0583	2.7.11.1	K14498	CAMK_CAMK_like.7 - CAMK includes calcium/calmodulin depedent protein kinases
MDC027871.11: 6913-8058	AT2G45260.1	PF04859					GIL1, putative
MDC032130.10: 2771-3287	AT1G08180.1						
MDC036854.6: 543-1070	AT2G46495.1	PF00097	PTHR22764				zinc finger, C3HC4 type domain containing protein
MDC002191.244: 5992-6164	AT5G47030.1	PF02823	PTHR13822	KOG1758	3.6.3.14	K02134	ATP synthase delta chain, mitochondrial precursor, putative
MDC036969.18: 8353-8496	AT1G15270.1	PF09072					coiled-coil domain-containing protein 72, putative
MDC040767.9: 10828-11034	AT3G02250.1	PF10250					auxin-independent growth promoter protein, putative
MDC002203.349: 4228-4862	AT1G62290.2	PF00026, PF03489, PF05184	PTHR13683	KOG1339	3.4.23.40	K08245	aspartic proteinase oryzasin-1 precursor, putative
MDC002205.555: 7793-8082	AT1G11910.1	PF00026, PF03489, PF05184	PTHR13683	KOG1339	3.4.23.40	K08245	aspartic proteinase oryzasin-1 precursor, putative
MDC002205.555: 8858-9031	AT1G62290.2	PF00026, PF03489, PF05184	PTHR13683	KOG1339	3.4.23.40	K08245	aspartic proteinase oryzasin-1 precursor, putative
MDC002205.604: 5796-6019	AT3G15351.2						expressed protein
MDC002252.327: 4583-5069	AT1G07520.1	PF03514					SCARECROW, putative
MDC002319.140: 10705-11101	AT2G38905.1	PF01679	PTHR21659	KOG1773			OsRCI2-7 - Putative low temperature and salt responsive protein
MDC000071.210: 1438-1573	AT4G16695.3						
MDC002360.331: 36076-36218	AT3G17760.2	PF00282	PTHR11999	KOG1383	4.1.1.15	K01580	decarboxylase, putative
MDC002367.269: 48264-48619	AT5G17330.1	PF00282	PTHR11999	KOG1383	4.1.1.15	K01580	glutamate decarboxylase, putative
MDC002367.269: 48993-49472	AT1G65960.2	PF00282	PTHR11999	KOG1383	4.1.1.15	K01580	glutamate decarboxylase, putative
MDC002367.269: 49581-49783	AT4G13195.1						
MDC002385.290: 19935-20648	AT4G13230.1		PTHR23241:SF11				
MDC002412.304: 11037-11650	AT5G19130.2	PF04114	PTHR13304	KOG3566		K05289	GPI transamidase component family protein, putative
MDC002431.300: 12026-12395	AT3G26510.5	PF00564					PB1 domain containing protein

MDC002441.272: 2839-3539	ATCG01250.1	PF00361	PTHR22773	KOG4668			NADPH-dependent oxidoreductase, putative
MDC002450.221: 3501-4098	AT3G17668.1						expressed protein
MDC002453.447: 10532-10849	AT3G18570.1	PF01277					oleosin, putative
MDC000298.380: 1328-1593	AT5G56630.1	PF00365	PTHR13697	KOG2440	2.7.1.11	K00850	6-phosphofructokinase, putative
MDC002536.231: 28261-28837	AT5G02520.1	PF09133					expressed protein
MDC002555.573: 6522-6894	AT2G38740.1	PF00702	PTHR18901	KOG2914			haloacid dehalogenase-like hydrolase family protein, putative
MDC002562.442: 3585-4052	AT2G38740.1	PF00702	PTHR18901	KOG2914			haloacid dehalogenase-like hydrolase family protein, putative
MDC002562.442: 4163-4526	AT2G38740.1	PF00702	PTHR18901	KOG2914			haloacid dehalogenase-like hydrolase family protein, putative
MDC002562.442: 4820-4968	AT2G38740.1	PF00702	PTHR18901	KOG2914			haloacid dehalogenase-like hydrolase family protein, putative
MDC002562.442: 5044-5170	AT3G12587.1	PF10215					expressed protein
MDC002563.449: 3601-3812	AT4G02290.1	PF00759	PTHR22298				endoglucanase, putative
MDC002579.350: 565-1558	AT1G07440.2	PF00106	PTHR19410	KOG0725			oxidoreductase, short chain dehydrogenase/reductase family protein, putative
MDC002584.153: 3776-3993	AT4G10840.1	PF07719, PF00515, PF07721	PTHR19959	KOG1840			tetratricopeptide repeat domain containing protein
MDC002655.565: 10635-11102	AT4G10840.1	PF07719, PF00515, PF07721	PTHR19959	KOG1840			tetratricopeptide repeat domain containing protein
MDC002655.586: 7567-8051	AT5G51700.1	PF04968	PTHR12621			K13458	rar1, putative
MDC002662.815: 1633-1925	AT4G19003.1	PF05871	PTHR13149	KOG4068		K12189	vacuolar protein-sorting-associated protein 25, putative
MDC002663.516: 8880-9798	AT3G12030.1	PF01956	PTHR20917	KOG3312			fb27, putative
MDC002683.322: 3279-3696	AT1G23440.1		PTHR23402	KOG4755			pyrrolidone-carboxylate peptidase, putative
MDC002758.275: 5034-5548	AT1G23440.1		PTHR23402	KOG4755			pyrrolidone-carboxylate peptidase, putative
MDC002758.275: 7054-7287	AT1G52570.1	PF00168, PF00614, PF12357	PTHR18896	KOG1329			phospholipase D, putative
MDC002787.258: 19523-20073	AT4G17690.1	PF00141			1.11.1.7	K00430	peroxidase family protein
MDC002848.461: 9691-10126	AT1G66950.1	PF00005, PF01061, PF08370	PTHR19241	KOG0065			pleiotropic drug resistance protein, putative
MDC000368.236: 1585-1999	AT2G01410.1						expressed protein
MDC002955.279: 38802-39101	AT1G19240.1						expressed protein
MDC002986.271: 21-529	AT1G02790.1	PF00295			3.2.1.67	K01213	polygalacturonase, putative
MDC003026.402: 4690-4972	AT2G15450.1	PF00295					polygalacturonase, putative
MDC003026.402: 5565-6093	AT5G65550.1		PTHR11926	KOG1192			glucosyltransferase, putative
MDC003081.405: 1372-1864	AT5G65550.1		PTHR11926	KOG1192			glucosyltransferase, putative
MDC003081.405: 1945-2200	AT4G21120.1	PF00324	PTHR11785	KOG1286			amino acid permease family protein, putative
MDC000368.238: 33490-34602	AT3G07760.2	PF00536					expressed protein
MDC003198.202: 2865-3190	AT5G53490.3	PF00805					thylakoid lumenal protein, putative
MDC003205.158: 29546-29798	AT5G53490.3	PF00805					thylakoid lumenal protein, putative
MDC003205.158: 29880-30320	AT2G46550.2						expressed protein

MDC003205.158: 76934-77309	AT1G30450.2	PF00324	PTHR11827	KOG2082			amino acid permease family protein, putative
MDC000368.238: 51135-51386	AT4G35100.2	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC003306.225: 3479-3782	AT2G16850.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC003306.225: 3868-4016	AT2G16850.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC003306.225: 4116-4489	AT3G02720.1	PF01965	PTHR11019	KOG2764			DJ-1 family protein, putative
MDC003313.350: 8410-8848	AT1G31817.1	PF00411	PTHR11759	KOG0408			ribosomal protein, putative
MDC003322.305: 8692-9506	AT4G21440.1	PF00249	PTHR10641	KOG0048		K09422	MYB family transcription factor, putative
MDC003396.159: 7266-7693	AT3G16340.2	PF01061, PF08370, PF00005	PTHR19241	KOG0065			pleiotropic drug resistance protein, putative
MDC003415.452: 48231-48632	AT5G18790.1	PF00471		KOG3505			50S ribosomal protein L33, putative
MDC003417.148: 4832-5225	AT2G02990.1	PF00445	PTHR11240	KOG1642			ribonuclease T2 family domain containing protein
MDC003465.666: 11182-11467	AT2G47680.1	PF00271, PF00642	PTHR18934	KOG0920			zinc finger helicase family protein, putative
MDC003476.424: 4739-5090	AT2G40370.1	PF07732, PF00394, PF07731	PTHR11709	KOG1263			laccase precursor protein, putative
MDC003534.362: 4332-4810	AT5G48640.1	PF00134	PTHR10026	KOG0794			cyclin, putative
MDC003623.656: 7835-8044	AT4G00585.1						expressed protein
MDC003652.401: 5479-5810	AT3G58560.1	PF03372	PTHR12121	KOG0620	3.1.-.-	K12603	endonuclease/exonuclease/phosphatase family domain containing protein
MDC003661.185: 20810-21803	AT5G08100.1	PF01112	PTHR10188	KOG1592	3.4.19.5	K13051	L-asparaginase precursor protein, putative
MDC003664.475: 11513-12117	AT5G08120.1						microtubule-associated protein, putative
MDC003664.475: 17093-17401	AT5G36110.1	PF00067	PTHR19383	KOG0157			cytochrome P450, putative
MDC003668.599: 3948-4504	AT5G36110.1	PF00067	PTHR19383	KOG0157			cytochrome P450, putative
MDC003668.599: 4608-4827	AT4G23420.3	PF00106	PTHR19410	KOG1208			oxidoreductase, short chain dehydrogenase/reductase family domain containing family
MDC003691.613: 12408-12611	AT4G23420.3	PF00106	PTHR19410	KOG1208			oxidoreductase, short chain dehydrogenase/reductase family domain containing family
MDC003691.613: 13105-13267	AT4G23420.3	PF00106	PTHR19410	KOG1208			oxidoreductase, short chain dehydrogenase/reductase family domain containing family
MDC003691.613: 14240-14582	AT2G18110.1	PF00736	PTHR11595	KOG1668		K03232	elongation factor protein, putative
MDC003707.256: 151-617	AT2G02720.1	PF04431, PF00544			4.2.2.2	K01728	pectate lyase precursor, putative
MDC000416.247: 35408-35747	AT1G11910.1	PF00026, PF03489, PF05184	PTHR13683	KOG1339	3.4.23.40	K08245	aspartic proteinase oryzasin-1 precursor, putative
MDC003743.404: 7074-7268	AT1G08230.2	PF01490	PTHR22950	KOG1303			transmembrane amino acid transporter protein, putative
MDC003758.352: 13113-13479	AT3G20600.1						harpin-induced protein 1 domain containing protein
MDC003785.419: 14126-14836	AT2G43780.2						conserved hypothetical protein
MDC003785.419: 15852-16189	AT3G20800.1	PF04078	PTHR12262	KOG3036		K12606	expressed protein
MDC003833.254: 923-1391	AT1G14420.1	PF04431, PF00544			4.2.2.2	K01728	pectate lyase precursor, putative
MDC000416.247: 35907-36548	AT5G66740.1	PF04788					expressed protein
MDC003876.694: 2083-2790	AT5G66740.1	PF04788					expressed protein
MDC003876.694: 3305-3512	AT1G13360.1						expressed protein

MDC003878.401: 325-1733	AT2G40470.1	PF03195					DUF260 domain containing protein, putative
MDC003882.313: 12016-12674	AT2G42760.1						expressed protein
MDC003889.426: 7020-7694	AT1G71010.1	PF01504	PTHR23086	KOG0230			1-phosphatidylinositol-4-phosphate 5-kinase/ zinc ion binding protein, putative
MDC000421.511: 6588-6935	AT2G01940.3	PF12171, PF00096	PTHR11389				ZOS8-07 - C2H2 zinc finger protein
MDC003936.406: 51932-52906	AT1G27530.1	PF08694	PTHR12921	KOG3357		K12165	ufm1-conjugating enzyme 1, putative
MDC003963.399: 2459-2839	AT1G48830.2	PF01251	PTHR11278	KOG3320			40S ribosomal protein S7, putative
MDC004009.559: 39608-40030	AT1G48830.2	PF01251	PTHR11278	KOG3320			40S ribosomal protein S7, putative
MDC004009.559: 40130-40478	AT1G48830.2	PF01251	PTHR11278	KOG3320			40S ribosomal protein S7, putative
MDC004009.559: 40660-40931	AT3G19760.1	PF00270, PF00271	PTHR10967	KOG0328	3.6.4.13	K13025	DEAD-box ATP-dependent RNA helicase, putative
MDC004010.194: 30326-30466	AT2G01970.1	PF02990	PTHR10766	KOG1277			transmembrane 9 superfamily member, putative
MDC004088.250: 961-1337	AT1G07830.1	PF06984, PF00831	PTHR21183	KOG3331			39S ribosomal protein L47, mitochondrial precursor, putative
MDC004095.243: 345-694	AT2G46150.1	PF03168					harpin-induced protein 1 domain containing protein
MDC004097.230: 13303-14099	AT3G54200.1	PF03168					harpin-induced protein 1 domain containing protein
MDC004097.232: 10956-11698	AT2G44360.1						
MDC004168.448: 5563-5714	AT2G17990.1						calcium-dependent protein kinase CPK1 adapter protein 2, putative
MDC004176.297: 3407-3797	AT1G07440.2	PF00106	PTHR19410	KOG0725			oxidoreductase, short chain dehydrogenase/reductase family protein, putative
MDC004279.272: 6053-6248	AT1G07440.2	PF00106	PTHR19410	KOG0725			oxidoreductase, short chain dehydrogenase/reductase family protein, putative
MDC004279.407: 7341-7593	AT2G29320.1	PF00106	PTHR19410	KOG0725	1.1.1.206	K08081	oxidoreductase, short chain dehydrogenase/reductase family domain containing protein
MDC004279.407: 8692-9013	AT5G48960.1	PF05761	PTHR12103	KOG2469			5-nucleotidase domain-containing protein, putative
MDC004302.250: 3053-3502	AT3G48140.1	PF06522					B12D protein, putative
MDC000479.396: 652-1113	AT5G18150.1		PTHR12133				expressed protein
MDC004356.237: 6421-6708	AT5G18150.1		PTHR12133				expressed protein
MDC004356.237: 6808-6910	AT5G59970.1	PF00125	PTHR10484	KOG3467		K11254	Core histone H2A/H2B/H3/H4 domain containing protein, putative
MDC004389.393: 4277-4752	AT5G04500.1	PF09258	PTHR11062	KOG1022			exostosin, putative
MDC004425.303: 2507-3293	AT2G46150.1	PF03168					harpin-induced protein 1 domain containing protein
MDC004475.200: 4627-5729	AT3G12870.1						expressed protein
MDC004559.262: 978-1347	AT3G25940.1	PF01096	PTHR11239	KOG2907	2.7.7.6	K03000	DNA-directed RNA polymerase I subunit RPA12, putative
MDC004588.262: 3095-3346	AT5G53070.1	PF01281	PTHR21368	KOG4607			ribosomal L9, putative
MDC004652.210: 27146-27473	AT1G11910.1	PF00026, PF03489, PF05184	PTHR13683	KOG1339	3.4.23.40	K08245	aspartic proteinase oryzasin-1 precursor, putative
MDC004719.334: 33353-33870	AT1G11910.1	PF00026, PF03489, PF05184	PTHR13683	KOG1339	3.4.23.40	K08245	aspartic proteinase oryzasin-1 precursor, putative
MDC004719.334: 35584-35741	AT1G02070.1						zinc finger protein, putative
MDC004742.548: 8028-8154	AT3G18215.1	PF04654					expressed protein

MDC004763.566: 3821-4013	AT5G18790.1	PF00471		KOG3505			50S ribosomal protein L33, putative
MDC004790.466: 18774-19119	AT1G05960.2		PTHR12444	KOG1877			cyclin-related protein, putative
MDC004812.214: 10140-10649	AT2G46590.2	PF02701					dof zinc finger domain containing protein, putative
MDC004894.273: 6281-6551	AT4G30380.1	PF03330					beta-expansin precursor, putative
MDC004903.290: 28-253	AT4G35783.1	PF08137					conserved hypothetical protein
MDC005044.363: 2733-3247	AT4G25260.1	PF04043					invertase/pectin methylesterase inhibitor family protein, putative
MDC005053.110: 4914-5359	AT5G62360.1	PF04043					invertase/pectin methylesterase inhibitor family protein, putative
MDC005053.110: 5464-5590	AT4G23100.3	PF04107			6.3.2.2	K01919	glutamate--cysteine ligase, putative
MDC005075.307: 3581-3994	AT2G29590.1	PF03061	PTHR21660	KOG3328			thioesterase family protein, putative
MDC005094.389: 2512-3049	AT2G06990.1	PF00270, PF00271, PF08148	PTHR11752	KOG0948			DSHCT domain containing protein
MDC005141.258: 7613-7859	AT5G49810.1		PTHR11751	KOG0257	2.1.1.12	K08247	methionine S-methyltransferase, putative
MDC005190.583: 11765-12203	AT5G20170.1						expressed protein
MDC005190.586: 28693-29117	AT3G06170.1	PF03348	PTHR10383	KOG2592			TMS membrane protein/tumour differentially expressed protein, putative
MDC005242.172: 12540-13598	AT5G66930.3	PF07855	PTHR13292	KOG4493			expressed protein
MDC005257.231: 6275-6378	AT5G53370.1	PF04043, PF01095	PTHR22931:SF5				pectinesterase, putative
MDC005334.309: 40809-41221	AT1G17020.1	PF03171	PTHR10209	KOG0143			naringenin,2-oxoglutarate 3-dioxygenase, putative
MDC000612.338: 24965-25404	AT4G17190.1	PF00348	PTHR11525	KOG0711	2.5.1.1, 2.5.1.10	K00787	polyprenyl synthetase, putative
MDC005353.186: 3030-3296	AT1G34750.1	PF00481	PTHR13832	KOG0698			protein phosphatase 2C, putative
MDC005367.75: 16852-17121	AT1G22280.3	PF00481	PTHR13832	KOG0698			protein phosphatase 2C, putative
MDC005367.75: 17253-17433	AT1G61070.1	PF07333, PF00304					DEF8 - Defensin and Defensin-like DEFL family
MDC005456.101: 32525-33076	AT3G14630.1	PF00067	PTHR19383	KOG0157			cytochrome P450 72A1, putative
MDC005483.475: 1862-2359	AT3G14630.1	PF00067	PTHR19383	KOG0157			cytochrome P450 72A1, putative
MDC005483.475: 2519-2878	AT5G56170.1						GPI-anchored protein, putative
MDC005607.185: 3202-3687	AT4G30790.1	PF10377	PTHR13222				expressed protein
MDC000651.338: 6690-7035	AT3G03520.1	PF04185			3.1.4.3	K01114	phosphoesterase family protein, putative
MDC005623.471: 5146-5546	AT1G13440.2	PF00044, PF02800	PTHR10836	KOG0657	1.2.1.12	K00134	glyceraldehyde-3-phosphate dehydrogenase, putative
MDC005648.396: 4843-5646	AT5G64610.1	PF11717, PF00385, PF01853	PTHR10615	KOG2747	2.3.1.48	K11308	MYST-like histone acetyltransferase 1, putative
MDC005683.152: 7464-7625	AT1G21630.1	PF00036	PTHR11216	KOG0998			EF hand family protein, putative
MDC005717.683: 79-577	AT1G05170.2	PF01762	PTHR11214	KOG2288			galactosyltransferase, putative
MDC005782.166: 27529-28337	AT5G15790.2	PF00097	PTHR22766				zinc finger, C3HC4 type domain containing protein
MDC005795.287: 6123-6431	AT2G39500.1						
MDC005856.445: 7345-7621	AT5G51190.1	PF00847					AP2 domain containing protein
MDC005866.401: 35521-36684	AT3G12360.1	PF00023	PTHR18958	KOG4412			ankyrin repeat-containing protein, putative

MDC005950.209: 1841-2991	AT3G12360.1	PF00023	PTHR18958	KOG4412			ankyrin repeat-containing protein, putative
MDC005950.237: 13639-14704	AT1G22070.1	PF00170, PF07716				K14431	transcription factor, putative
MDC000667.347: 25394-25851	AT3G49590.3	PF10033		KOG4573			expressed protein
MDC006166.69: 22399-22979	AT1G71865.1						expressed protein
MDC006167.203: 6785-7413	AT5G51280.1	PF00270, PF00271, PF00098	PTHR10967	KOG0341	3.6.4.13	K13116	DEAD-box ATP-dependent RNA helicase 35A, putative
MDC006191.181: 59671-60011	AT1G19130.1	PF06172				K09705	cupin superfamily protein, putative
MDC006200.189: 255-378	AT1G19130.1	PF06172				K09705	cupin superfamily protein, putative
MDC006200.189: 719-977	AT3G61770.1	PF02681					Divergent PAP2 family domain containing protein
MDC006204.278: 5342-5722	AT1G33055.1						expressed protein
MDC006212.350: 19119-19764	AT1G05810.1	PF00071, PF08477	PTHR11708	KOG0087		K07976	ras-related protein, putative
MDC006231.909: 29746-30018	AT3G28050.1	PF00892					auxin-induced protein 5NG4, putative
MDC006246.466: 8563-8734	AT1G23440.1		PTHR23402	KOG4755			pyrrolidone-carboxylate peptidase, putative
MDC006260.462: 6583-6877	AT2G45960.3	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC006289.408: 8288-8577	AT4G00430.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC006289.408: 9216-9268	AT4G27750.1						impaired sucrose induction 1, putative
MDC006289.410: 4115-4432	AT2G37750.1						
MDC006340.216: 19210-20061	AT1G26670.1	PF05008, PF12352	PTHR21230	KOG1666		K08493	vesicle transport v-SNARE protein, putative
MDC006363.247: 28792-29092	AT5G49525.1						expressed protein
MDC006424.194: 9322-9729	AT1G67620.1	PF02410	PTHR21043	KOG3212			expressed protein
MDC006471.130: 167-359	AT4G14103.2	PF00646, PF07723					OsFBL3 - F-box domain and LRR containing protein
MDC006517.413: 12768-13371	AT1G65000.1						expressed protein
MDC006520.239: 5991-6735	AT2G31085.1						
MDC006520.258: 40616-41227	AT2G26740.1	PF12146, PF00561	PTHR10992	KOG4178			hydrolase, alpha/beta fold family domain containing protein
MDC006603.356: 888-1307	AT3G04180.1	PF00190, PF07883					Cupin domain containing protein
MDC006603.734: 7137-7471	AT1G67830.1	PF00657					GDSL-like lipase/acylhydrolase, putative
MDC006603.753: 648-986	AT5G59960.1						expressed protein
MDC006624.226: 615-886	AT5G59970.1	PF00125	PTHR10484	KOG3467		K11254	Core histone H2A/H2B/H3/H4 domain containing protein, putative
MDC006624.226: 6675-7194	AT3G19760.1	PF00270, PF00271	PTHR10967	KOG0328	3.6.4.13	K13025	DEAD-box ATP-dependent RNA helicase, putative
MDC006639.149: 9374-9510	AT3G19760.1	PF00270, PF00271	PTHR10967	KOG0328	3.6.4.13	K13025	DEAD-box ATP-dependent RNA helicase, putative
MDC006639.149: 10169-10560	AT3G13530.1	PF00069, PF07714, PF00514, PF02985	PTHR22986	KOG0198			STE_MEKK_ste11_MAP3K.1 - STE kinases include homologs to sterile 7, sterile 11 and sterile 20 from yeast
MDC006639.149: 10658-11039	AT4G17560.1	PF01245	PTHR15680	KOG1698			50S ribosomal protein L19, putative
MDC006675.305: 292-384	AT5G47190.1	PF01245	PTHR15680	KOG1698			50S ribosomal protein L19, putative
MDC006675.305: 1240-1535	AT3G54820.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative

MDC006710.363: 6328-6707	AT3G54820.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC006710.363: 6868-6988	AT2G37170.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC006710.363: 8904-9171	AT3G54820.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC006710.363: 9415-9810	AT5G09960.1	PF05627					expressed protein
MDC006772.187: 518-757	AT5G51190.1	PF00847					AP2 domain containing protein
MDC000706.497: 11725-12685	AT2G28840.2	PF00023	PTHR18958	KOG4214			ankyrin repeat domain-containing protein 28, putative
MDC006804.119: 728-1335	AT1G08230.2	PF01490	PTHR22950	KOG1303			transmembrane amino acid transporter protein, putative
MDC006834.195: 5931-6204	AT1G09900.1	PF01535	PTHR10483				pentatricopeptide repeat domain containing protein, putative
MDC007047.426: 19297-19639	AT5G47820.2	PF00225	PTHR16012	KOG0244		K10395	kinesin motor domain containing protein, putative
MDC007057.148: 1220-1518	AT4G22570.1	PF00156		KOG1712	2.4.2.7	K00759	phosphoribosyl transferase, putative
MDC007058.290: 9956-10075	AT5G16380.1	PF04398					expressed protein
MDC007066.597: 3722-4200	AT2G39970.1	PF00153	PTHR11896	KOG0769		K13354	mitochondrial carrier protein, putative
MDC007117.619: 30844-31444	AT5G23070.1	PF00265	PTHR11441	KOG3125	2.7.1.21	K00857	thymidine kinase, putative
MDC007192.252: 1298-1688	AT3G06980.1	PF00270, PF00271	PTHR10967	KOG0331			DEAD-box ATP-dependent RNA helicase, putative
MDC007239.507: 18593-18889	AT1G74340.1	PF07297		KOG3488		K09658	dolichol phosphate-mannose biosynthesis regulatory protein, putative
MDC000741.237: 17856-18144	AT5G19140.2	PF12481, PF12504	PTHR11772				stem-specific protein TSJT1, putative
MDC007283.1041: 967-1726	AT3G57080.1	PF03871, PF01191	PTHR10535	KOG3218			DNA-directed RNA polymerases I, II, and III subunit RPABC1, putative
MDC007283.917: 10694-10994	AT1G56070.1	PF00009, PF01926, PF03144, PF03764, PF00679	PTHR23115	KOG0469	3.6.5.3	K03234	elongation factor, putative
MDC007289.107: 9052-9887	AT5G02490.1	PF00012	PTHR19375	KOG0100		K03283	DnaK family protein, putative
MDC007308.338: 25153-25355	AT5G35910.1	PF01612, PF00570	PTHR12124	KOG2206	3.1.13.-	K12591	3-5 exonuclease family protein, putative
MDC007315.261: 46384-46703	AT5G61670.2						OR, putative
MDC007344.1025: 7310-7666	AT4G25620.1						expressed protein
MDC000796.524: 10939-12475	AT4G09550.1	PF12554					expressed protein
MDC007350.839: 8348-8675	AT2G28680.1	PF00190					cupin domain containing protein
MDC007376.494: 17698-18125	AT2G28680.1	PF00190					cupin domain containing protein
MDC007376.494: 18463-18905	AT1G07750.1	PF00190					cupin domain containing protein
MDC007376.494: 18965-19412	AT3G12700.1		PTHR13683	KOG1339			aspartyl protease family protein, putative
MDC007422.177: 2747-3819	AT3G12700.2		PTHR13683				aspartyl protease family protein, putative
MDC007422.177: 4802-5629	AT5G11760.1	PF08576					expressed protein
MDC007454.249: 3101-3502	AT1G75620.1	PF07250, PF09118					glyoxal oxidase-related, putative
MDC007469.326: 38450-38743	AT5G62000.4	PF02362, PF06507, PF02309					auxin response factor, putative
MDC007485.683: 834-1172	AT2G43370.1	PF00076	PTHR13952	KOG0113		K13155	RNA recognition motif containing protein, putative
MDC007509.254: 671-866	AT5G41800.1	PF01490	PTHR22950	KOG1303			transmembrane amino acid transporter protein, putative

MDC000812.292: 23436-23602	AT4G22720.2	PF00814	PTHR11735	KOG2708	3.4.24.57	K01409	O-sialoglycoprotein endopeptidase, putative
MDC007568.248: 14938-15506	AT4G22720.2	PF00814	PTHR11735	KOG2708	3.4.24.57	K01409	O-sialoglycoprotein endopeptidase, putative
MDC007568.248: 16771-17120	AT2G40470.1	PF03195					DUF260 domain containing protein, putative
MDC007582.375: 15700-16040	AT4G19185.1	PF00892					nodulin, putative
MDC007598.175: 7142-7412	AT4G19185.1	PF00892					nodulin, putative
MDC007598.175: 13744-13944	AT1G31500.4	PF03372	PTHR12121	KOG0620			endonuclease/exonuclease/phosphatase family domain containing protein
MDC007614.448: 8696-9035	AT3G23600.2	PF01738	PTHR17630	KOG3043			endo-1,3;1,4-beta-D-glucanase precursor, putative
MDC007624.239: 4383-4761	AT5G41800.1	PF01490	PTHR22950	KOG1303			transmembrane amino acid transporter protein, putative
MDC000812.292: 23731-24364	AT2G01480.1	PF10250					growth regulator related protein, putative
MDC007641.311: 4854-5781	AT4G32300.1	PF01453, PF00069, PF07714	PTHR23258	KOG1187			lectin protein kinase family protein, putative
MDC007651.256: 7095-7497	AT2G18030.1	PF01625	PTHR10173	KOG1635			peptide methionine sulfoxide reductase, putative
MDC007657.717: 4681-5123	AT5G42960.1						DANA2, putative
MDC007713.205: 2812-3135	AT4G13195.1						
MDC007725.313: 21618-22339	AT1G11170.1	PF05212					lysine ketoglutarate reductase trans-splicing related 1, putative
MDC007736.142: 17091-17712	AT4G30770.1						expressed protein
MDC000813.771: 2702-3359	AT1G74530.3						expressed protein
MDC007790.237: 180-282	AT2G02090.1	PF00176, PF00271	PTHR10799	KOG0389	3.6.4.12	K14439	SNF2 family N-terminal domain containing protein
MDC007791.237: 10017-10398	AT1G76900.2	PF00646, PF01167	PTHR16517	KOG2502			OsFBT7 - F-box and tubby domain containing protein
MDC007792.401: 10562-11508	AT2G33730.1	PF00270, PF00271	PTHR10967	KOG0333	3.6.4.13	K12858	DEAD-box ATP-dependent RNA helicase, putative
MDC007792.401: 29323-29673	AT4G08770.1	PF00141			1.11.1.7	K00430	peroxidase precursor, putative
MDC007858.422: 10539-10754	AT5G05340.1	PF00141			1.11.1.7	K00430	peroxidase precursor, putative
MDC007858.422: 12370-12964	AT2G47900.3	PF00646, PF01167	PTHR16517	KOG2502			OsFBT5 - F-box and tubby domain containing protein
MDC007953.177: 16669-16974	AT1G12410.1	PF00574	PTHR10381	KOG0840	3.4.21.92	K01358	OsClp9 - Putative Clp protease homologue
MDC008045.226: 5778-6105	AT3G61430.2	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC008099.122: 14997-15532	AT4G23400.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC008099.122: 15720-15853	AT4G00300.2	PF11721					receptor-like protein kinase At3g46290 precursor, putative
MDC000814.336: 7471-7949	AT1G01620.2	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC008099.122: 15946-16282	AT4G00430.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC008099.122: 16388-16809	AT5G40240.2	PF00892		KOG1441			auxin-induced protein 5NG4, putative
MDC008104.97: 4350-4465	AT5G40230.1	PF00892					auxin-induced protein 5NG4, putative
MDC008104.97: 4893-5080	AT3G17490.1	PF00646, PF07734					OsFBX464 - F-box domain containing protein
MDC008108.99: 7464-9223	AT2G34340.1	PF04520					DUF584 domain containing protein, putative
MDC008119.473: 1280-1805	AT2G24100.1						expressed protein
MDC008177.674: 13219-13664	AT4G12710.1	PF00514	PTHR23316	KOG4646			armadillo/beta-catenin repeat family protein, putative

MDC008184.205: 8772-9239	AT1G54540.1	PF03168					harpin-induced protein 1 domain containing protein
MDC008212.498: 491-1195	AT1G69410.1	PF00467, PF01287	PTHR11673	KOG3271		K03263	eukaryotic translation initiation factor 5A, putative
MDC008233.164: 1510-1669	AT4G02420.1	PF00139, PF00069, PF07714	PTHR23258	KOG1187			receptor like protein kinase, putative
MDC008313.318: 4207-4571	AT1G74530.3						expressed protein
MDC008325.354: 8874-8959	AT5G17760.1	PF00004	PTHR23070	KOG0743			mitochondrial chaperone BCS1, putative
MDC008336.464: 6231-7078	AT4G28210.1						
MDC008345.348: 4511-4874	AT5G47470.1	PF00892					integral membrane protein DUF6 domain containing protein
MDC008453.913: 10123-10374	AT4G21800.2	PF03029	PTHR21231	KOG1532		K06883	ATP binding protein, putative
MDC008485.183: 6542-7083	AT5G42965.1						conserved hypothetical protein
MDC008496.393: 3311-4214	AT5G47180.2	PF00635	PTHR10809	KOG0439			MSP domain containing protein
MDC008501.186: 4780-5080	AT2G24100.1						expressed protein
MDC008511.144: 10693-11189	AT4G10360.2	PF03798	PTHR13439	KOG4561			transmembrane protein 56, putative
MDC008521.354: 1690-2152	AT1G06650.2	PF03171	PTHR10209	KOG0143			1-aminocyclopropane-1-carboxylate oxidase homolog 2, putative
MDC000835.215: 2033-2459	AT1G30970.2		PTHR23215	KOG2893			ZOS9-19 - C2H2 zinc finger protein
MDC008558.180: 22776-23209	AT5G27770.1	PF01776	PTHR10064	KOG3434		K02891	60S ribosomal protein L22-2, putative
MDC008575.351: 1527-1902	AT5G27770.1	PF01776	PTHR10064	KOG3434		K02891	60S ribosomal protein L22-2, putative
MDC008575.351: 2734-2941	AT5G41330.1	PF02214	PTHR11145	KOG2714			B4-BTB4 - Bric-a-Brac, Tramtrack, Broad Complex BTB domain with B4 subfamily conserved sequence
MDC008579.487: 3510-3869	AT1G71950.1	PF05922	PTHR10795				subtilisin N-terminal Region family protein
MDC008657.482: 3281-3527	AT4G12020.3	PF02671, PF03106, PF00931, PF07725, PF00560, PF00069, PF07714	PTHR22986	KOG0198			STE_MEKK_ste11_MAP3K.12 - STE kinases include homologs to sterile 7, sterile 11 and sterile 20 from yeast
MDC008801.230: 1128-1609	AT1G07510.1	PF06480, PF00004, PF01434	PTHR23076	KOG0731	3.4.24.-	K08956	OsFtsH8 FtsH protease, homologue of AtFtsH3/10
MDC008815.152: 3297-3548	AT1G50670.1	PF02338	PTHR13312		3.1.2.-	K13719	OTU-like cysteine protease family protein, putative
MDC008844.652: 13597-13959	AT1G20430.1		PTHR21568				expressed protein
MDC008880.141: 64155-64719	AT2G36985.1	PF08137					expressed protein
MDC008909.172: 124-491	AT1G20980.1	PF03110					OsSPL15 - SBP-box gene family member
MDC008927.255: 16667-17470	AT5G66780.1						expressed protein
MDC008947.382: 12415-12822	AT1G30760.1	PF01565, PF08031	PTHR11748				reticuline oxidase-like protein precursor, putative
MDC000845.305: 5283-5857	AT1G11910.1	PF00026, PF03489, PF05184	PTHR13683	KOG1339	3.4.23.40	K08245	aspartic proteinase oryzasin-1 precursor, putative
MDC008968.446: 15847-16400	AT4G31750.1	PF00481	PTHR13832	KOG0698			protein phosphatase 2C, putative
MDC009079.262: 4671-4942	AT4G31750.1	PF00481	PTHR13832	KOG0698			protein phosphatase 2C, putative
MDC009079.262: 6115-6244	AT4G31750.1	PF00481	PTHR13832	KOG0698			protein phosphatase 2C, putative
MDC009079.262: 7239-7401	AT1G25510.1		PTHR13683	KOG1339			aspartic proteinase, putative
MDC000851.382: 15529-16034	AT5G40230.1	PF00892					auxin-induced protein 5NG4, putative

MDC009088.260: 67-301	AT3G28050.1	PF00892					auxin-induced protein 5NG4, putative
MDC009088.260: 680-830	AT3G28050.1	PF00892					auxin-induced protein 5NG4, putative
MDC009088.260: 987-1845	AT4G37270.1	PF00122, PF00702	PTHR11939	KOG0207			cadmium/zinc-transporting ATPase, putative
MDC009100.743: 18942-19318	AT5G58950.1	PF07714, PF00069	PTHR23257	KOG0192			protein kinase domain containing protein
MDC009128.602: 32330-32740	AT2G23090.1	PF04419					expressed protein
MDC009154.309: 1280-1387	AT3G60210.1	PF00166	PTHR10772	KOG1641			chaperonin, putative
MDC009197.269: 132-321	AT1G24260.3	PF00319, PF01486	PTHR11945	KOG0014			OsMADS7 - MADS-box family gene with MIKCc type-box
MDC009276.331: 6201-6936	AT1G58120.1						CPuORF38 - conserved peptide uORF-containing transcript
MDC009282.275: 3906-4729	AT1G16900.1	PF03901	PTHR22760	KOG2515	2.4.1.-	K03846	Alg9-like mannosyltransferase protein, putative
MDC009291.126: 1104-1457	AT5G59970.1	PF00125	PTHR10484	KOG3467		K11254	Core histone H2A/H2B/H3/H4 domain containing protein, putative
MDC009303.382: 1557-1878	AT1G51060.1	PF00125, PF00808	PTHR23430	KOG1756		K11251	core histone H2A/H2B/H3/H4, putative
MDC000876.364: 2401-2783	AT5G38200.1	PF07722					
MDC009325.280: 310-749	AT2G39730.1	PF00004		KOG0651			AAA-type ATPase family protein, putative
MDC009368.188: 2702-3008	AT5G36930.2	PF01582, PF00560, PF00931, PF07725	PTHR23155	KOG4658			disease resistance protein RGA3, putative
MDC009423.544: 1637-2373	AT2G17420.1	PF07992, PF00070	PTHR22912	KOG0404	1.8.1.9	K00384	thioredoxin reductase 2, putative
MDC009436.50: 32007-32411	AT3G45140.1	PF01477, PF00305	PTHR11771		1.13.11.12	K00454	lipoxygenase, putative
MDC009458.215: 14228-14402	AT5G56670.1	PF04758	PTHR12650	KOG0009		K02983	expressed protein
MDC009483.38: 3322-3461	AT5G47310.1	PF05903	PTHR12378	KOG0324			ethylene-responsive element-binding protein, putative
MDC009489.259: 582-956	AT5G47310.1	PF05903	PTHR12378	KOG0324			ethylene-responsive element-binding protein, putative
MDC009489.259: 2379-2689	AT5G47310.1	PF05903	PTHR12378	KOG0324			ethylene-responsive element-binding protein, putative
MDC009489.375: 2207-2531	AT2G23570.1						OsPOP4 - Putative Prolyl Oligopeptidase homologue
MDC009490.558: 6365-6741	AT2G31600.1						expressed protein
MDC009501.247: 2219-2729	AT4G16143.2	PF01749, PF00514, PF02985, PF03130	PTHR23316	KOG0166			importin subunit alpha, putative
MDC009595.146: 45-416	AT3G14430.1						expressed protein
MDC009596.264: 70-344	AT2G20290.1	PF02736, PF00063, PF00612, PF01843	PTHR13140	KOG0160			myosin, putative
MDC009602.113: 10106-10498	AT1G71950.1	PF05922	PTHR10795				subtilisin N-terminal Region family protein
MDC009615.292: 631-756	AT4G38790.1	PF00810	PTHR10585	KOG3106			ER lumen protein retaining receptor, putative
MDC009626.195: 1302-1624	AT5G41760.2	PF04142	PTHR10231	KOG2234			UAA transporter family domain containing protein
MDC000140.134: 54551-54847	AT5G10180.1	PF00916, PF01740	PTHR11814	KOG0236			sulfate transporter, putative
MDC009685.334: 6702-7096	AT1G75460.1	PF02190	PTHR23327	KOG4159			ATP-dependent protease, putative
MDC009708.152: 51041-51699	AT5G40150.1	PF00141			1.11.1.7	K00430	peroxidase family protein
MDC000908.450: 4034-4471	AT3G04730.1	PF02309					OsIAA30 - Auxin-responsive Aux/IAA gene family member
MDC009814.418: 6273-6657	AT4G17690.1	PF00141			1.11.1.7	K00430	peroxidase family protein

MDC000908.450: 4523-5057	AT4G14550.1	PF02309					OsIAA30 - Auxin-responsive Aux/IAA gene family member
MDC009814.418: 7581-7800	AT3G28430.1	PF09758	PTHR21481	KOG2219			expressed protein
MDC009830.368: 4257-4492	AT5G65780.1	PF01063	PTHR11825	KOG0975	2.6.1.42	K00826	aminotransferase domain containing protein, putative
MDC009850.21: 558-987	AT1G19580.1	PF00132	PTHR22572	KOG4042			bacterial transferase hexapeptide domain containing protein
MDC009856.139: 35298-35913	AT1G06990.1	PF00657	PTHR22835:SF27				GDSL-like lipase/acylhydrolase, putative
MDC009859.245: 7701-7947	AT1G16180.2	PF03348	PTHR10383	KOG2592			TMS membrane protein/tumour differentially expressed protein, putative
MDC009907.294: 23684-23868	AT1G16180.2	PF03348	PTHR10383	KOG2592			TMS membrane protein/tumour differentially expressed protein, putative
MDC009907.294: 24320-24561	AT1G16180.2	PF03348	PTHR10383	KOG2592			TMS membrane protein/tumour differentially expressed protein, putative
MDC009907.294: 24876-25099	AT4G34700.1	PF05347	PTHR12868	KOG3466	1.6.5.3, 1.6.99.3	K03965	LYR motif containing protein, putative
MDC009946.417: 4427-4703	AT5G37600.1	PF03951, PF00120	PTHR20852	KOG0683	6.3.1.2	K01915	glutamine synthetase, catalytic domain containing protein
MDC009950.283: 2248-2601	AT1G66200.3	PF03951, PF00120	PTHR20852	KOG0683			glutamine synthetase, catalytic domain containing protein
MDC009950.283: 3474-3584	AT5G37600.1	PF03951, PF00120	PTHR20852	KOG0683	6.3.1.2	K01915	glutamine synthetase, catalytic domain containing protein
MDC009950.283: 3884-4023	AT5G37600.1	PF03951, PF00120	PTHR20852	KOG0683	6.3.1.2	K01915	glutamine synthetase, catalytic domain containing protein
MDC009950.283: 4266-4401	AT5G16570.1	PF03951, PF00120	PTHR20852	KOG0683	6.3.1.2	K01915	glutamine synthetase, catalytic domain containing protein
MDC009950.288: 5596-6266	AT5G32470.1	PF03070	PTHR20858				TENA/THI-4 family protein, putative
MDC009976.359: 12472-13055	AT5G32470.1	PF03070	PTHR20858				TENA/THI-4 family protein, putative
MDC009976.359: 13136-13571	AT2G36070.1	PF04280	PTHR10721	KOG2580			tim44-like domain containing protein
MDC009991.166: 1671-1911	AT4G23160.1	PF07727, PF01657, PF00069, PF07714, PF11883	PTHR11439	KOG1187			TKL_IRAK_DUF26-lc.20 - DUF26 kinases have homology to DUF26 containing loci
MDC009992.373: 5233-5529	AT5G02230.2	PF00702	PTHR18901	KOG3109			haloacid dehalogenase-like hydrolase family protein, putative
MDC010058.303: 36260-36547	AT5G41800.1	PF01490	PTHR22950	KOG1303			transmembrane amino acid transporter protein, putative
MDC010065.349: 3326-3668	AT2G22640.1					K05752	BRICK1, putative
MDC010071.397: 392-525	AT1G56700.3		PTHR23402	KOG4755			pyrrolidone-carboxylate peptidase, putative
MDC000997.260: 16008-16410	AT4G16450.2						expressed protein
MDC010085.172: 13-504	AT3G10050.1	PF00291, PF00585	PTHR10314	KOG1250	4.3.1.19	K01754	threonine dehydratase biosynthetic, putative
MDC010099.229: 4737-5125	AT5G06700.1	PF03005					leaf senescence related protein, putative
MDC010104.1012: 30864-31577	AT2G32000.2	PF01751, PF01131	PTHR11390	KOG1957	5.99.1.2	K03165	DNA topoisomerase 3 protein, putative
MDC010172.365: 23895-24342	AT2G37170.1	PF00230	PTHR19139	KOG0223		K09872	aquaporin protein, putative
MDC010185.231: 6884-7177	AT1G56700.3		PTHR23402	KOG4755			pyrrolidone-carboxylate peptidase, putative
MDC000997.260: 17123-17228	AT3G50590.1	PF00400	PTHR12816				WD domain, G-beta repeat domain containing protein
MDC010186.403: 23504-23954	AT5G26800.1	PF09597					expressed protein
MDC010192.333: 5522-5655	AT3G12360.1	PF00023	PTHR18958	KOG4412			ankyrin repeat-containing protein, putative
MDC010192.348: 12503-13571	AT5G62790.2	PF02670, PF08436			1.1.1.267	K00099	1-deoxy-D-xylulose 5-phosphate reductoisomerase, putative
MDC010200.476: 4261-4691	AT5G62790.2	PF02670, PF08436			1.1.1.267	K00099	1-deoxy-D-xylulose 5-phosphate reductoisomerase, putative

MDC010200.476: 4901-5052	AT5G51970.2	PF08240, PF00107	PTHR11695	KOG0024	1.1.1.14	K00008	dehydrogenase, putative
MDC010241.223: 17213-18085	AT1G23440.1		PTHR23402	KOG4755			pyrrolidone-carboxylate peptidase, putative
MDC000997.260: 17440-17768	AT5G40350.1	PF00249	PTHR10641	KOG0048		K09422	MYB family transcription factor, putative
MDC010252.317: 1021-1375	AT5G64360.4	PF00226	PTHR11821				heat shock protein DnaJ, putative
MDC010254.244: 14459-14910	AT3G56150.2	PF05470, PF01399	PTHR13937	KOG1076		K03252	eukaryotic translation initiation factor 3 subunit C, putative
MDC010268.425: 12245-12627	AT3G42860.1	PF06839, PF00098	PTHR23002	KOG4400			GRF zinc finger family protein
MDC010300.238: 15044-16078	AT3G55640.1	PF00153	PTHR11896	KOG0752			mitochondrial carrier protein, putative
MDC010318.100: 9492-9884	AT3G19080.1	PF08766, PF02201	PTHR13844	KOG1946			upstream activation factor subunit spp27, putative
MDC010319.227: 8072-8321	AT1G49820.1	PF01636					methylthioribose kinase, putative
MDC010325.233: 4683-4903	AT1G48300.1						expressed protein
MDC010328.213: 18449-19160	AT1G62290.2	PF00026, PF03489, PF05184	PTHR13683	KOG1339	3.4.23.40	K08245	aspartic proteinase oryzasin-1 precursor, putative
MDC010328.215: 28204-28446	AT3G46890.1						expressed protein
MDC010431.261: 2731-2961	AT2G19080.1		PTHR12289	KOG3028			expressed protein
MDC010441.401: 17991-18191	AT5G49525.1						expressed protein
MDC010450.908: 6750-7226	AT1G08530.1						expressed protein
MDC010450.949: 3543-4321	AT5G45970.1	PF00071, PF08477	PTHR11708	KOG0393		K07975	ras-related protein, putative
MDC001007.507: 15632-16109	AT2G02130.1	PF07333, PF00304					DEF8 - Defensin and Defensin-like DEFL family
MDC010466.196: 24-204	AT5G56170.1						GPI-anchored protein, putative
MDC010492.245: 666-1340	AT5G36110.1	PF00067	PTHR19383	KOG0157			cytochrome P450, putative
MDC010598.348: 9370-9523	AT1G32340.1	PF05773, PF00097, PF01485	PTHR11685	KOG1814	6.3.2.19	K11971	ara54-like RING finger protein, putative
MDC010640.116: 5178-5493	AT4G12760.1						expressed protein
MDC010687.251: 5882-6163	AT4G21810.1	PF04511	PTHR11009	KOG0858			Der1-like family domain containing protein
MDC010697.307: 4965-5070	AT4G35790.1	PF00168, PF00614, PF12357	PTHR18896	KOG1329			phospholipase D, putative
MDC010709.414: 585-1037	AT1G02090.3	PF01399	PTHR15350	KOG3250		K12180	proteasome subunit, putative
MDC010751.335: 5076-5282	AT5G27870.1	PF04043, PF01095, PF04886					pectinesterase, putative
MDC010779.408: 15723-16139	AT3G61060.1	PF00646					OsFBX391 - F-box domain containing protein
MDC010783.139: 10332-11071	AT3G61060.1	PF00646					OsFBX391 - F-box domain containing protein
MDC010783.139: 11498-12068	AT1G49700.2	PF09713					plant-specific domain TIGR01589 family protein, putative
MDC010817.271: 27525-27737	AT3G15360.1	PF00085	PTHR10438	KOG0910			thioredoxin, putative
MDC010842.294: 4654-4752	AT1G15520.1	PF00005, PF01061, PF08370	PTHR19241	KOG0065			pleiotropic drug resistance protein, putative
MDC010937.194: 12046-12338	AT5G66900.1	PF05659, PF00931, PF00560	PTHR23155	KOG4658			disease resistance protein, putative
MDC010969.378: 7112-8073	AT3G51430.2	PF03088	PTHR10426	KOG1520			strictosidine synthase, putative
MDC001040.307: 555-1041	AT4G14960.2	PF00091, PF03953	PTHR11588	KOG1376		K07374	tubulin/FtsZ domain containing protein, putative
MDC001048.310: 7356-8038	AT3G15630.1						expressed protein

MDC011163.587: 1351-1663	AT3G51000.1	PF12146, PF00561	PTHR10992	KOG4178			hydrolase, alpha/beta fold family domain containing protein
MDC011167.337: 32-262	AT5G48100.1	PF07732, PF00394, PF07731	PTHR11709	KOG1263			laccase precursor protein, putative
MDC011283.393: 3854-4077	AT3G21610.2	PF02681					Divergent PAP2 family domain containing protein
MDC011325.298: 41258-41415	AT3G51240.1	PF03171	PTHR10209	KOG0143	1.14.11.9	K00475	naringenin,2-oxoglutarate 3-dioxygenase, putative
MDC011373.244: 3946-4433	AT3G51240.2	PF03171	PTHR10209	KOG0143	1.14.11.9	K00475	naringenin,2-oxoglutarate 3-dioxygenase, putative
MDC011373.244: 4627-5027	AT3G51240.2	PF03171	PTHR10209	KOG0143	1.14.11.9	K00475	naringenin,2-oxoglutarate 3-dioxygenase, putative
MDC011373.244: 5822-6338	AT4G09830.1						holocarboxylase synthetase, putative
MDC011377.138: 14053-14246	AT4G09830.1						holocarboxylase synthetase, putative
MDC011377.138: 16729-17502	AT1G22790.2						expressed protein
MDC011377.138: 23384-24008	AT1G34000.1						high light inducible protein, putative
MDC011377.138: 30623-31125	AT1G34000.1						high light inducible protein, putative
MDC011377.138: 31736-32194	AT1G72730.1	PF00270, PF00271	PTHR10967	KOG0327		K03257	DEAD-box ATP-dependent RNA helicase, putative
MDC011423.269: 13482-14391	AT1G54270.2	PF00270, PF00271	PTHR10967	KOG0327		K03257	DEAD-box ATP-dependent RNA helicase, putative
MDC011423.269: 14495-14923	AT5G20350.1	PF00023, PF01529	PTHR22883	KOG0509			palmitoyltransferase TIP1, putative
MDC011475.283: 13870-14453	AT1G69450.2	PF02714	PTHR13018	KOG1134			DUF221 domain containing protein
MDC011493.183: 13848-14159	AT4G23330.2						

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Curriculum vitae

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2009-2013	PhD in phytopathology, plant sciences, University of Zurich, Prof. Dr. Beat Keller, and Agroscope Wädenswil (Switzerland), Bacteriology group, Dr. Brion Duffy
2008	Master of science in biology, plant sciences, at the Institute of Plant Biology, University of Zurich, Prof. Dr. Beat Keller Lab
2007	Bachelor of science in biology, University of Zurich
2002-2006	Basic course of biology, University of Zurich (second intermediate diploma)

Publications

Tim Kamber, Theresa A. Lansdell, Virginia O. Stockwell, Carol A. Ishimaru, Theo H.M. Smits and Brion Duffy. Characterization of the antibacterial peptide herbicolin I biosynthetic operon in *Pantoea vagans* biocontrol strain C9-1 and incidence in *Pantoea* species. (Applied and Environmental Microbiology, AEM.07351-11; 78:4412-4419).

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Erwinia species reveals the presence of putative effector islands that may be translocated by the VgrG and Hcp proteins. (BMC Genomics. 2011; 12: 576)

Theo H. M. Smits, Fabio Rezzonico, **Tim Kamber**, Jochen Blom, Alexander Goesmann, Carol A. Ishimaru, Jürg E. Frey, Virginia O. Stockwell, and Brion Duffy. Metabolic versatility and antibacterial metabolite biosynthesis are distinguishing genomic features of the fire blight antagonist *Pantoea vagans* C9-1. (PLoS One. 2011; 6(7): e22247)

Theo H. M. Smits, Fabio Rezzonico**, Tim Kamber**, Alexander Goesmann, Carol A. Ishimaru, Virginia O. Stockwell, Jürg E. Frey, and Brion Duffy**.** Genome sequence of the biocontrol agent *Pantoea vagans* strain C9-1 (Journal of Bacteriology. 2010; 24: 6486-6487)

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Theo H. M. Smits, Sebastian Jaenicke, Fabio Rezzonico, **Tim Kamber**, Alexander Goesmann, Jürg E Frey, and Brion Duffy. Complete genome sequence of the fire blight pathogen *Erwinia pyrifoliae* DSM 12163T and comparative genomic insights into plant pathogenicity (BMC Genomics. 2010; 11: 2)

Oral presentations:

Tim Kamber, Theo Smits , Brion Duffy. Functional analysis of *Erwinia Amylovora* type VI secretion systems. 12th International Workshop on Fire Blight, 2010, Warsaw

Theo Smits, Fabio Rezzonico, **Tim Kamber**, Alexander Goesmann, Jürg Frey, Brion Duffy. Evolutionary insights from *Erwinia Amylovora* genomics. 12th International Workshop on Fire Blight, 2010, Warsaw

Posters:

Tim Kamber, Theresa Lansdell, Theo Smits, Virginia Stockwell, Carol Ishimaru, Brion Duffy. Characterizarion of the antibacterial peptide herbicolin I biosynthetic operon in the fire blight biocontrol agent *Pantoea vagans* C9-1. 12th International Workshop on Fire Blight, 2010, Warsaw

Theo Smits, Fabio Rezzonico, Cosima Pelludat, **Tim Kamber**., Carol Ishimaru, Jürg Frey, Alexander Goesmann, Virginia Stockwell, Brion Duffy. Complete genome sequence analysis of *Pantoea vagans* biocontrol strain C9-1. 12th International Workshop on Fire Blight, 2010, Warsaw

Theo Smits, Fabio Rezzonico, **Tim Kamber**, Jochen Blom, Alexander Goesmann, Jürg Frey, Brion Duffy. Complete Genome Sequence of the Fire Blight Pathogen Erwinia amylovora. The 5th Swiss Molecular Microbiology Meeting 2010